University of Alberta

Stress and mortality of four boreal tree species following variable retention harvesting

by

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Abstract

Variable retention (VR) harvesting involves the preservation of live and dead trees within the boundaries of the harvested area, to emulate the distribution of trees following wildfire or other natural disturbances. The living remnant forest structures are believed to provide the regenerating stand with a biological legacy from the previous stand to achieve a broad array of forest management objectives; most importantly, maintenance of biological diversity and ecosystem integrity. Recent observations of VR cutovers have shown that retention trees often die shortly after the harvest, raising concerns that some of the objectives of VR could be compromised. Thus, the purpose of this research was to quantify the mortality rates of white spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.) residuals in boreal mixedwood VR cutovers. Mortality rates in VR plots were 2.5- to 4-fold greater than in control plots for all species. I hypothesized that atmospheric water stress, due to the abrupt change in microclimate following harvest, was the causal reason for this mortality. Accordingly, this study also examined the microclimate before and immediately after VR harvesting, and investigated the differential species responses in transpiration rates (Q_l). Nearly 3-fold increases in potential evapotranspiration (ET_P) in the VR site produced greater Q_l for spruce (2.5-times) and birch (1.6-times), but only marginal increases in Q_l for poplar. This suggested stomatal closure by the poplar and birch residuals, likely to prevent xylem cavitation and diminished hydraulic conductivity. Total water potential (Ψ) of twigs also indicated water stress in poplar and birch in the VR site. Measurements of the carbon isotope ratios ($\delta^{13}C$) in stem wood from aspen before and after VR provided

additional evidence of atmospheric moisture stress in residual trees. The $\delta^{13}C$ was also found to be greater in trees from drier regions, indicating that atmospheric water stress in residuals, potentially leading to dieback and mortality, is likely to be a greater issue in drier regions. Species differences in susceptibility to cavitation, combined with differences in stress-coping mechanisms and physiology, appeared to influence the response in Q_l and $\delta^{13}C$ to elevated ET_P following VR harvesting.

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List of Symbols and Abbreviations

^{12}C	Carbon isotope 12
^{13}C	Carbon isotope 13
A_L	leaf area (m^2)
A_s	sapwood cross-sectional area (cm^2)
Aw	trembling aspen (*Populus tremuloides* Michx.)
Bw	paper birch (*Betula papyrifera* Marsh.)
C	control trees
c_a	heat capacity of air ($J\ kg^{-1}\ K^{-1}$)
CC	crown class
CD	co-dominant crown class
C_p	specific heat of dry air at constant pressure ($J\ kg^{-1}\ K^{-1}$)
D	vapour pressure deficit (Pa)
D	dominant crown class
dbh	diamter at breast height (1.3 m)
E	edge trees
e_a	ambient vapour pressure (Pa)
e_s	saturation vapour pressure (Pa)
ET_P	potential evapotranspiration ($m\ s^{-1}$)
g_a	aerodynamic conductance ($m\ s^{-1}$)
g_c	canopy conductance ($m\ s^{-1}$)
g_s	stomatal conductance
htlc	height to live crown (m)
IR	isolated residual trees
K_Ψ	hydraulic conductivity ($m^{-2}\ Pa^{-1}\ s^{-1}$)
L	length (m)
LCR	live crown ratio (%)
m	annual mortality rate (% trees year^{-1})
m_d	total dry biomass (kg)
N	Nitrogen
N_0	total number of trees
N_t	total number of dead trees
Pb	balsam poplar (*Populus balsamifera* L.)
PSP	permanent sample plot

Q	volumetric flow ($m^3\ s^{-1}$)
Q^*	net radiation ($W\ m^{-2}$)
Q_d	total daily volumetric water use ($m^3\ day^{-1}$)
Q_{h}	hydraulic capacity ($m^4\ Pa^{-1}\ s^{-1}$) under a unit hydraulic gradient
Q_l	transpiration rate per unit leaf area ($m^3\ m^{-2}\ s^{-1}$)
Q_{L}	leaf specific hydraulic capacity ($m^{-2}\ Pa^{-1}\ s^{-1}$)
$Q_{l\text{-}max}$	maximum transpiration rate per unit leaf area ($m^3\ m^{-2}\ s^{-1}$)
RH	relative humidity
SC	slenderness coefficient (tree height/dbh)
SLA	specific leaf area/ one-sided leaf area per unit dry biomass ($m^2\ kg^{-1}$)
Sw	white spruce (*Picea glauca* (Moench) Voss)
t	time interval
T_a	air temperature (°C or K)
u	wind speed ($m\ s^{-1}$)
U	understorey/suppressed crown class
u_*	friction velocity ($m\ s^{-1}$)
V	crown volume (m^3)
VR	variable retention
v_s	mean sap flux density ($m\ s^{-1}$)
z_o	roughness length (m)
γ	psychrometric constant ($Pa\ K^{-1}$)
Δ	slope of the saturation vapour pressure vs. temperature curve ($Pa\ K^{-1}$)
$\delta^{13}C$	carbon isotope ratio ($^{13}C/^{12}C$) with respect to Pee Dee Belemnite (PDB) standard
ΔT	temperature difference between heated and unheated sap flow probes (°C)
ΔT_M	maximum temperature difference between sap flow probes (°C)
$\Delta\Psi$	water potential difference across a sample (Pa)
ε	Δ/γ
θ_v	volumetric moisture content (%)
κ	von Karman's constant (turbulent momentum exchange coefficient)
λ_υ	latent heat of vaporization ($J\ kg^{-1}$)
ρ_a	density of air ($kg\ m^{-3}$)
ρ_ω	density of water ($kg\ m^{-3}$)
Ψ	total water potential (Pa)
Ω	decoupling coefficient

Chapter 1

INTRODUCTION

1.1 THE BOREAL FOREST

The boreal forest is the most widespread terrestrial biome or environmental community in the world, constituting approximately 32% of the Earth's forests and covering over 14 million km^2 (Burton et al. 2003). It forms a circumpolar belt of coniferous dominated forests throughout the cold northern climates of Europe, Asia and North America. The mean minimum temperature is often below 0°C for a period of 6 to 8 months, while the mean temperature may be above 10°C for a period of 3 to 5 months (Woodward 1995). The majority of precipitation falls during the summer and may range from 300 to 1400 mm. As the single largest land-based ecosystem, it covers approximately 35 – 40% of Canada's land mass (roughly one-tenth of the world's forests), extending from Newfoundland to Yukon. It has some of the most immense unpopulated landscapes on Earth, interwoven with large rivers, lakes, and wetlands. These forests are dominated by four genera of conifers (*Picea*, *Pinus*, *Abies*, and *Larix*) and four genera of hardwoods (*Populus*, *Betula*, *Alnus*, and *Salix*) (Larsen 1990, Graham and Jain 1998). The wood is slow-growing and uniform with exceptional qualities for pulp and paper, structural panelling (plywood and oriented strandboard) and dimensional lumber (Bowyer et al. 2003). Thus, boreal forest ecosystems contain a wealth of timber and non-timber values including wood fibre supply, recreation, wilderness areas, wildlife habitat and ecosystem services (i.e. carbon sequestration, soil protection, microclimate moderation, preservation of watershed function). The natural wealth of Canada's boreal sustains many Aboriginal communities, supports close to 400,000 direct jobs in silviculture, logging, wood industries, paper and allied products, as well as hundreds of thousands (~770,000) of indirect jobs through the purchase of its goods and services (NRC 2005). As Canada's largest natural resource industry, forestry in the boreal forest contributes billions of dollars to the Canadian economy each year. Thus, Canada has both local and global responsibilities to manage its forests in a sustainable manner.

However, in the last several decades, there has been a dramatic increase in the rate of forest exploitation to meet expanding societal demands for goods and services (Karlin 1995, Burton et al. 2003). Although forestry is the primary industry, mining, oil and gas extraction, hunting, trapping, fishing, tourism and recreation also contribute to the mounting stress placed on the finite natural resources of the boreal forest. Consequently, forest habitats, flora, and fauna have been degraded and depleted throughout Canada and the world (Perry 1998, Ericsson et al. 2005). This has motivated recognition of the importance of managing and developing these resources with an approach that strives to maintain biodiversity and long-term ecosystem productivity (Franklin 1993, Freedman et al. 1994, Christensen et al. 1996, Bridge et al. 2005).

1.2 SUSTAINABILITY AND ECOSYSTEM-BASED MANAGEMENT

More than 50 years ago, the visionary philosopher, forester, wildlife manager, professor, conservationist, and author Aldo Leopold wrote about the need to enlarge "the boundaries of the community to include the soils, waters, plants, and animals, or collectively: the land. A land ethic of course cannot prevent the alteration, management, and use of these 'resources,' but it does affirm their right to continued existence, and, at least in spots, their continued existence in a natural state" (Leopold 1949). The Kenyan proverb: "We do not inherit the earth from our parents, we borrow it from our children" also embodies the idea of an environmental or land ethic (Pezzoli 1997). However, only recently has broad public awareness and concern for the wise uses of our natural resources become more prominent. An ecosystem approach to land management, as implied by Leopold, was not earnestly supported by scientists, managers and others until the late 1980's (Grumbine 1994). The concept of sustainable development emerged during this period in an attempt to explore the relationship between development and the environment (Banerjee 2003). Over 70 definitions of sustainable development now exist (Holmberg and Sandbrook 1992). However, the most widely accepted definition was provided by the Brundtland Commission, who defined sustainable development as "development that meets the needs of the present without compromising the ability of future generations to meet their own needs" (WCED 1987). Since then, there has been a proliferation of the discussion of sustainability and sustainable development by government and others concerned with the management of forests (CCFM 1992, 1998, Adamowicz and Burton 2003, NFSC 2003). Coincidently, there has been an immense expansion of the knowledge of how ecosystems function. Combined with greater societal expectations for improved stewardship of our forests, this improved knowledge has changed the way we perceive, study, and manage our natural resources (Galindo-Leal and Bunnell 1995). Thus, there has been a noticeable paradigm shift in the attitude of the forest industry, away from intensive management designed to maximize wood production on all managed lands, towards a more holistic view of forest management on a portion of the land area; one that considers the social, economic and ecological values of forests, commonly known as the 'three pillars' of sustainability (Brunson 1993, Rowe 1994, Goodland 1995).

The paradigm shift in forest management has led to rapid modifications of silvicultural methods, which are now regularly designed to achieve a balance between timber production and preservation of natural ecosystems (Gillis 1990, Swanson and Franklin 1992, Spence 2001). Over the past decade, our evolving, yet somewhat fragmented, knowledge of natural disturbance dynamics has primarily formed the basis for new forest management policy and management approaches (Attiwill 1994, Lieffers et al. 1996, Bergeron and Harvey 1997, Angelstam 1998, DeLong 2002). The underlying assumption is that the organisms of a forest are probably best adapted to the natural disturbance regimes of forest ecosystems with which they have survived and evolved over millenia and, thus should cope more easily with the ecological changes produced by forest management activities if the pattern and structure created are similar to those of natural disturbance (Hunter 1993, Haila et al. 1994, DeLong and Tanner 1996, Gauthier et al. 1996, Bergeron et al. 1999).

1.3 VARIABLE RETENTION (VR)

The natural disturbance regime varies greatly across the boreal forest; however, the principle disturbances are wildfire (Rowe and Scotter 1973, Johnson 1992, Bergeron et al. 2001) and insect outbreaks (Blais 1983, Morin 1994, Hogg et al. 2002), while wind storms, ice storms, snow breakages, and diseases play a lesser role in stand-replacing disturbances (Chen and Popadiouk 2002). Because fire is predominantly the major disturbance, occurring with a frequency of 30 to 500 years (depending on the species and climate), policy and management approaches have focussed on maintaining stand composition and structures similar to those that characterize this type of disturbance.

Research has shown that forest fires seldom, if ever, kill all vegetation within the main fire perimeter (Eberhart and Woodard 1987, DeLong and Tanner 1996). Typically, following wildfires, there are fire skips (i.e. groups of unburned trees and snags) remaining within the burned area. Consequently, the silvicultural system termed "variable retention" (also known as: green-tree retention, partial retention, snag retention, biological legacy retention or clearcutting with reserves) was designed to retain individual trees or groups of trees to preserve structural elements of the harvested stand for at least one rotation, so that specific management objectives may be achieved (Franklin et al. 1997). Those objectives typically include enhanced conservation of biological diversity at the stand level by providing the new stand with a legacy from the previous stand (North et al. 1996, Chambers et al. 1999, Progar et al. 1999, Zenner 2000). Specifically, this practice is believed to maintain canopy continuity and enhance structural complexity by the preservation of old and large trees, provide diversity in microhabitats (vertically and horizontally) for species dependent on either living trees or snags, provide refugia for various organisms, maintain pre-harvest stand-level diversity, improve connectivity between landscape elements, while reducing initial impacts and speeding long-term forest recovery (Franklin et al. 1997, Schieck and Hobson 2000; Zenner 2000; Vanha-Majamaa and Jalonen 2001, Sullivan et al. 2001).

Owing to its immense potential, variable retention has been widely adopted throughout the boreal forests in Canada, Europe and Scandinavia, as well as in the Pacific Northwest. In the United States, the federal forest management policy currently requires that 15% of a cutover contains live residual trees (USDA and USDI 1994). Further, 70% of the residuals must be aggregated in 0.2 – 1.0 ha patches, while the remainder are dispersed as small groups (<0.2 ha) or as isolated trees. In European countries, such as Sweden, there have also been policy directives from the state for forest managers to increase retention of live trees to 5% to maintain biodiversity (Fries et al. 1997). In Canada, the guidelines for VR harvesting have been developed by the provinces and/or individual Forest Management Agreement (FMA) holders (DeLong 2002). For instance, the provinces of Alberta (ASRD 2006), British Columbia (BC Ministry of Forests 1995) and Ontario (OMNR 2001) have developed guidelines for VR designed to meet stand- and landscape-level biodiversity objectives, but only require less than 1% of the pre-harvest trees to be retained as live residuals within harvest areas. Nevertheless, individual FMA holders in these provinces have set their own guidelines for retention levels that range from 3 – 20% of merchantable timber, depending on the philosophies and objectives of the company (ALPAC 1996, Weyerhaeuser Edson Forestlands 1997, Sougavinski and Doyon 2003).

However, the guidelines for VR have been primarily developed based on professional judgement, often using knowledge obtained from forests outside of the region in which they were implemented. The guidelines are largely untested scientific hypotheses, which require a more rigorous analysis to ensure sustainable management of boreal forests (Spence 2001). Presently, due to minimal practical experience and scientific research, the ecological ramifications of VR harvesting practices are poorly understood. Given the complexity of natural ecosystems, it is not surprising that our knowledge on the ecological and biological diversity effects of this relatively new silvicultural practice is limited. Since knowledge in this area is incomplete, it is uncertain if the broad ranges of objectives that have been established for VR are attainable, or whether they are being compromised with the current practices. If attempts to manage the boreal forest in a sustainable manner are to be successful, forest management decisions must be more scientific based. Consequently, multidimensional empirical research is necessary to define ecosystem responses to the stresses associated with VR and to design acceptable environmental protection programs and resource management policies

1.4 KNOWLEDGE GAPS IN THE APPLICATION OF VR

A fundamental knowledge gap regarding VR is the post-harvest response and fate of retention trees. While it has been acknowledged that mortality of residual trees could be a concern in some regions (Franklin et al. 1997), there has been no research to assess this potential problem. A high rate of premature mortality of residuals shortly after VR harvest could provide complex challenges for land managers to meet certain objectives. While dead trees provide important structural inputs to the recovering site, much of the desired function or utility provided by mature, living trees could be lost from the site before the regenerating stand is able to replace those values. If the primary objectives of VR harvesting are to provide critical habitat elements, ameliorate microclimate change, enhance connectivity for movement of organisms, or to sustain certain basic ecosystem functions (Franklin et al. 2002), then high mortality rates could provide a key hindrance to sustainable forest management.

If forest management decisions are to be sustainable, it is imperative that we advance the knowledge of the fundamental processes governing premature mortality of trees in VR efforts. Retention trees may be exposed to increased environmental stress from altered microclimate, including increased fluctuations in wind speed (u), air temperature (T_a), relative humidity (RH), vapour pressure deficit (D) and net radiation (Q^*) (Cadenasso et al. 1997, Man and Lieffers 1999, Proe et al. 2001), producing greater evaporative demand in harvested areas (Zheng et al. 2000). These stresses could eventually lead to death of intolerant species. It is hypothesized that the atmospheric drought (high evaporative demand) surrounding the crowns of residual trees could cause partial or complete cavitation of the xylem (Jones and Sutherland 1991, Sperry and Pockman 1993, Nardini and Salleo 2000). This would limit the ability of the tree to deliver water to the leaves. Inadequate water supply to the foliage would ultimately reduce photosynthesis, leading to branch die-back and potentially whole tree mortality (Kobe and Coates 1997, Roy et al., 2001).

1.5 OVERVIEW OF STUDIES

To ensure that the practice of variable retention harvesting is meeting the objectives of land managers and to assist in the further development of sustainable silvicultural practices, it is critical to understand the post-harvest response of residual trees to this anthropogenic disturbance. Observations of widespread residual tree mortality shortly after variable retention logging in the boreal forest, has raised concerns that the desired legacy objectives of the land managers may be compromised. The hypothesis was that water stress could be the causal reason for this mortality. Thus, the principal objective of this dissertation was to explore the mortality rates of residual trees for several important boreal tree species. Further, I assessed how this mortality may be influenced by the physiological response (e.g. transpiration rates, carbon isotope discrimination) of the various species to the abrupt change in microclimate that could occur after VR harvest.

The objectives of Chapter 2 were to quantify the mortality rates of trembling aspen, balsam poplar, paper birch and white spruce dispersed residual trees five years after VR harvesting, and compare them with the natural mortality rates. I also examined whether residual mortality could be predicted by tree characteristics, such as crown class (CC), diameter-at-breast-height (dbh), tree height, slenderness coefficient (SC), diameter increment or damage to the lower bole that can occur during the harvest. I hypothesized that all species would have greater mortality rates in the VR plots than in the control plots. I also hypothesized that the mortality rates would be higher for dominant, taller, more slender trees and trees with greater harvesting damage.

In Chapter 3, I compared the change in microclimate and tree water relations between a boreal mixedwood, VR harvested stand and an adjacent, unharvested control stand. In both stands I measured air temperature (T_a), relative humidity (RH), vapour pressure deficit (D), net radiation (Q^*), wind speed (u) and soil volumetric moisture content (θ_v) before and after the VR harvest. These variables were used to calculate potential evapotranspiration (ET_P) at the crown level. Whole-tree sap flow response to ET_P and the individual micrometeorological variables was measured in white spruce, balsam poplar and paper birch with thermal-dissipation sap flow sensors. I hypothesized that all species of residual trees would experience greater transpiration rates and increased water stress due to elevated T_a, D, u and Q^* and decreased RH following partial harvesting. However, I anticipated greater differences in transpiration rates between the VR site and the control site for the hardwoods, poplar and birch, than for spruce.

Chapter 4 describes results of a field study designed to provide additional evidence of water stress in residual trees following VR harvesting. The study assessed the stable carbon isotope ratios ($\delta^{13}C$) of wood samples from trembling aspen trees in Drayton Valley and Calling Lake, Alberta and in Lac Duparquet, Quebec. Samples were collected from closed canopy/control (C), edge (E), and isolated residual (IR) positions from 7 replicated plots in each region. I hypothesized that discrimination against ^{13}C would be ranked as: C > E > IR trees. I also investigated if VR would subject residual trees to greater stress in drier regions by analysing the differences in $\delta^{13}C$ across a continental precipitation gradient. I anticipated that trees in the most xeric region (i.e. Calling Lake) would have greater $\delta^{13}C$, and more water stress, than trees from the most mesic region (i.e. Lac Duparquet). Finally, I examined whether slender or stout trees would show greater signs of stress following VR. I hypothesized that slender trees would have greater $\delta^{13}C$ than stout trees because of the greater potential for slender trees to suffer xylem damage from increased wind exposure and bending stress.

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Chapter 2

ELEVATED MORTALITY OF RESIDUAL TREES FOLLOWING VARIABLE RETENTION HARVESTING OF MIXEDWOOD FORESTS[1]

2.1 INTRODUCTION

Variable retention (VR) harvesting involves the preservation of large, mature trees in dispersed or aggregated patterns throughout forest cutovers. This coarse filter forest management strategy is an attempt to closely mimic the structural outcomes of natural disturbance (i.e. fire). It is assumed to sustain ecosystem functions and biological diversity at the stand level (Franklin et al. 1997, Zenner 2000, Bergeron et al. 2002). Thus, VR harvesting has recently been widely promoted and adopted as a management technique in boreal and temperate forest ecosystems (Bergeron and Harvey 1997, Fries et al. 1997, Franklin et al. 2002, Mitchell and Beese 2002). However, since the policies and guidelines of this harvesting practice have been developed predominantly from expert opinion (Halpern et al. 2005), many details regarding how to best implement VR are still unclear.

A potential problem that could compromise the benefits of residual trees on the structure, function and composition of the recovering forest is an accelerated rate of mortality shortly after cutting. Retention trees are exposed to increased environmental stress from greater evaporative demand, wind exposure and high soil moisture relative to trees in the intact forest (Adams et al. 1991; Franklin et al. 1997; Bladon et al. In press). Species that are sensitive to these stresses could eventually die. Several authors, primarily examining Douglas-fir dominated forests of the Pacific Northwest, have noted increased mortality of retention trees following VR harvesting (Adler 1994; Franklin et al. 2002; Walter and Maguire 2004). However, mortality of retention trees has been quantified only for a few species and regions. Additionally, the majority of studies have focused on mortality due to blowdown, resulting from wind exposure after partial harvesting (Arnott and Beese 1997; Franklin et al. 1997; Beurmeyer and Harrington 2002; Scott and Mitchell 2005). Thus, the rates of mortality after VR harvesting, in addition to the general issue of standing mortality (i.e. snag creation) after VR harvesting, remain poorly understood. Furthermore, little is known if structural characteristics of trees could be used to predict the probability of mortality. It has also been noted that logging damage to residual trees can be extensive, and could lead to increased mortality (Cline et al. 1991; Hartsough 2003). However, to my knowledge there have been no attempts to quantify mortality rates of residual trees due to machine damage in VR systems.

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The objectives were to quantify mean annual rates of mortality of residual trees for trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marsh.), and white spruce (*Picea glauca* (Moench) Voss) following VR cuts in boreal mixedwood stands, and compare these to the mortality rates for these species in undisturbed stands. I hypothesized that mortality rates for all species would be greater in VR plots than control plots. Additionally, I investigated whether mortality of residual trees could be related to factors such as crown class, diameter-at-breast-height (dbh), tree height, slenderness coefficient (height/dbh), and damage to the lower bole as a result of the harvest. Other authors have previously noted relationships between stress and/or mortality with increasing tree height, crown class and slenderness (Coates 1997; Ruel et al. 2000; Liu et al. 2003). Thus, I hypothesized that dominant, taller, more slender trees and trees with greater harvesting damage would have higher mortality rates.

2.2 MATERIALS AND METHODS

2.2.1 Study Site Descriptions

Initial surveys were conducted one year after variable retention harvesting of boreal mixedwood sites near Drayton Valley and Rocky Mountain House, Alberta, Canada, in the Lower Foothills Natural Subregion (52° 61′ and 53° 09′N and 114° 96′ and 115° 32′W). All sites were summer harvested by the same contractor. Site elevation ranged from approximately 800 – 1200 m with rolling topography and gentle slopes. The dominant soil types in the region were Orthic and Brunisolic Grey Luvisols. Climate is subhumid and continental, with long, cold winters and mild summers. The mean annual temperature is 2.3°C, with a mean monthly summer (May to August) temperature of 12.8°C, and a mean monthly winter (November to February) temperature of -7.8°C. Mean annual precipitation is 535 mm, with the majority (~77%) falling as rain during summer.

2.2.2 Field Sampling

In May 2001, 60 independent sampling plots (100-metre radius) were established within one-year-old variable retention cut-blocks (~1 – 10 % retention) containing primarily dispersed individuals. A dispersed individual was considered to be any tree that was isolated on the landscape or in a small patch of less than 10 trees. Plot centers were randomly established with the outer boundary a minimum of 200 m away from the outer boundary of any other plot, and the nearest suitable trees were then selected. Plots were distributed in VR areas covering 433.3 ha, spread over 27 sections. If present, one healthy residual tree from each species (trembling aspen, balsam poplar, paper birch and white spruce) and each crown class was chosen within each plot. Crown class was identified as either dominant (D), co-dominant (CD), or understory (U). The trees were categorized based upon their size relative to the adjacent stand; D trees possessed crowns that were in the upper canopy at the time of harvest, while CD trees were slightly shorter, with narrower crowns than D trees. Trees under the canopy at the time of harvest were classified as U. Trees displaying signs of pathogens, insect defoliation, crown dieback or stem form defects were not included. The GPS location and measurements of independent variables, including diameter-at-breast-height (dbh; 1.3 m), percent live crown and damage from harvesting as a percentage of the circumference of the bole were recorded for each tree. A total of 471 residual trees, or approximately 40 trees from each species and crown class were identified for survey (Table 2-1).

Sites were revisited in May 2005, after a period of 4 years, to evaluate tree condition and/or mortality. Each tree was assigned a condition code, adapted from McCune et al. (1988): 0 = healthy tree, all leaves present; 1 = weakened, but mostly healthy, minimal crown dieback (<20%); 2 = declining, heavy crown dieback (>20%), small twigs intact; 3 = full crown dieback, dead tree. Dead trees were further categorized similar to Senecal et al. (2004) to provide some indication of the different forms of mortality, where: 1 = snag (dead tree, still standing); 2 = broken after death; 3 = broken when alive (trees that were bent, snapped or crushed by other trees); 4 = uprooted (trees that blew over exposing the root system). I distinguished between trees in the dead tree categories 2 and 3 by examining the degree of decomposition and wood structural differences at the point of breakage. The presence of fine branches and leaves, no discoloration of wood and splintering or uneven/jagged wood at the point of breakage were indicative of trees that were broken when alive.

I measured tree height and height-to-live-crown from all standing trees using a Vertex III hypsometer (Haglöf Sweden AB, Langsele, Sweden). I also measured dbh and collected two estimates of crown radius, which were averaged for analysis. Slenderness coefficient was calculated as the ratio of tree height/dbh. Tree age was determined from increment cores extracted from all trees with a dbh > 20 cm. Cores were used to determine tree age. In the laboratory, cores were air dried and glued to grooved, wooden blocks with cores oriented so that xylem tracheary elements were at a right angle with the block surface. Cores were hand sanded, progressively using finer grit sandpaper and finally buffed with a lamb's wool pad to remove sawdust from the xylem vessels (Phipps 1985). Decayed wood prevented precise aging of many of the trees.

The natural mortality rates of all four species were determined from the long-term permanent sample plot (PSP) data collected by the Alberta Land and Forest Service since the early 1960s. The data were collected from 699 locations from a range of stand ages, densities, compositions and site conditions. A subset of plots with similar composition, age, elevation, slope and location (between 52° 42′ and 53° 33′N and 115° 10′ and 115° 71′W) as my study plots were used to estimate the natural mortality rate. Trees with broken tops, open scars, pronounced crooks, severe leans or with stem form defects in their first year of measurement were also removed from the data set. The final analysis was performed using 29 plots within mature stands, containing 9806 trees. The natural mortality rate for each species was estimated for each plot, and then averaged across all plots.

2.2.3 Mortality Rate Calculation

The mean annual mortality rate was calculated for each species and each plot separately. It was also determined for the three crown classes and for classes of slenderness coefficient. The mean annual mortality rate (*m*) was calculated as:

Equation 2-1

$$m = \left[\left(\frac{N_t}{N_0} \right) / t \right] \times 100$$

where N_t represents the number of dead trees, N_0 is the total number of stems and t is the time interval (years).

2.2.4 Statistical analyses

One-tailed t-tests, using plot as the experimental unit, were conducted to determine whether the mortality rates of the VR trees were significantly greater than the natural mortality rates for each of the four species, and to compare diameter increment (2001 – 2005) between living and dead residuals for each species. Crown class and slenderness coefficient (by crown class) effects on mortality were analyzed by a generalized mixed linear model, PROC GLIMMIX (Littell et al. 2006), for a randomized complete block design with no covariates. Multiple comparisons tests among crown classes were made with the Tukey test. Logistic regression, using PROC LOGISTIC (SAS Institute Inc. 1999) was used to determine, 1) if mortality was greater among trees damaged during harvest than among undamaged trees and 2) if the probability of mortality increased with increasing proportion of circumference damaged. In all analyses, the critical value for statistical significance was p=0.05.

2.3 RESULTS

Four years after the initial survey of VR harvested sites (in the period 1 to 5 years post-VR harvest), 42.3% of poplar, 34.3% of birch, 23.7% of aspen and 13.0% of spruce residuals were found dead, either as snags or as downed trees. The mean annual mortality rates (*m*) were 10.2% year^{-1} for poplar, 8.7% year^{-1} for birch, 6.1% year^{-1} for aspen and 2.9% year^{-1} for spruce (Figure 2-1). Compared to mortality rates in similar control plots (PSPs), average *m* for poplar in the VR plots was 4.3 times greater ($P < 0.0001$), for aspen 3.6 times greater ($P < 0.0001$), for birch 2.8 times greater ($P = 0.001$) and for spruce was 2.5 times greater ($P = 0.019$).

Of the trees still alive 5 years after the partial harvest, 17.8% of aspen, 36.1% of birch, 28.5% of poplar and 5.2% of spruce residuals were categorized as declining, with extensive crown dieback (Figure 2-2). An additional 11.8% of aspen, 19.4% of birch, 8.5% of poplar and 8.7% of spruce in the VR sites showed evidence of weakening, with low to moderate crown dieback. This suggests that all of the species may suffer additional mortality in future years.

There were strong differences between the deciduous species and spruce in the cause of mortality in the VR sites. The majority of dead residual aspen (75.7%), birch (69.4%) and poplar (92.7%) were found as standing dead (snags) (Figure 2-3). An additional 16.2% of aspen and 8.3% of birch were found broken, either before or after death. Few aspen (2.7%), birch (8.3%) and poplar (3.6%) died due to windthrow. In contrast, 80.0% of the dead spruce had been uprooted due to windthrow.

The factors related to mortality of the spruce that died, either due to windthrow or as standing mortality, were crown class and bole damage. Dominant spruce in VR sites were most likely to die (m = 6.9% year^{-1}), followed by co-dominants (m = 2.8% year^{-1}) and then understory residuals (m = 1.7% year^{-1}). If the bole of a residual spruce tree was damaged during the harvesting it was more likely to die shortly after VR than an undamaged tree ($P = 0.04$). Additionally, the frequency of mortality increased as the percentage of the circumference of the bole that was damaged increased ($P = 0.04$). Tree boles were damaged on 44.8% of spruce residuals. For trees that died, the mean extent of damage to the bole was 24.0% of the circumference of the tree, while an average of 13.2% of the bole was damaged in surviving spruce residuals.

The analyses of poplar residuals indicated that the probability of mortality increased with greater slenderness for both U ($P = 0.02$) and CD trees ($P = 0.03$). However, neither crown class or harvesting damage were significant predictors for poplar residual mortality. For the birch residuals, there was a significant relationship between crown class and mortality ($P = 0.04$). Multiple comparisons tests indicated that U birch were more likely to die post-VR than CD birch residuals. Additionally, the mortality of U birch was positively related to increasing slenderness coefficient (*P* = 0.04). For aspen residuals, crown class was a significant predictor of mortality (*P* = 0.05). Multiple comparisons tests indicated that CD aspen were significantly more likely to die post-VR than D aspen residuals.

There were strong differences in the percentage increase in diameter (2001 – 2005) between living and dead residuals for all 4 species (Figure 2-4). In general, surviving residuals of all species had a significantly greater increase in dbh after VR harvesting than residuals that died shortly after VR ($P < 0.01$).

2.4 DISCUSSION

This study showed strongly elevated mortality rates (*m*) of dispersed residual trees following variable retention (VR) harvesting of boreal mixedwood stands (Figure 2-1). The broadleaf residuals, balsam poplar (10.2% year^{-1}), paper birch (8.7% year^{-1}) and trembling aspen (6.1% year^{-1}), were the most vulnerable species to crown dieback and whole-tree mortality. Annual *m* of these species was 3- to 4-times greater in the VR plots than in control plots. Whether this is considered an acceptable level of mortality will likely depend on the forest management objectives. For instance, if VR harvest prescriptions are designed to maintain biological legacies that facilitate "lifeboating" of species and processes or to enhance connectivity (Franklin et al. 2002), then high rates of mortality could compromise such objectives, since the living, mature trees are likely to be lost before the regenerating stand will be able to replace their structural characteristics. Conversely, if snag creation is a priority, my results indicate that retention of isolated hardwood individuals (69.4 – 92.7% of dead trees were found standing) is more likely to provide this necessary ecological function, rather than conifers.

To my knowledge, this study is the first outside of the Pacific Northwest to demonstrate elevated mortality rates of retention trees following VR harvesting. However, there was a much higher rate of mortality in my plots than in other VR or partial-cut stands. In the Pacific Northwest, mortality of Douglas-fir (*Pseudotsuga menziesii* (Mirb.)) residuals ranged from 0.6 – 3.1% year^{-1}, with the majority of death due to windthrow (Adler 1994, Beurmeyer and Harrington 2002, Walter and Maguire 2004). Studies on shelterwood cutting and recently exposed riparian buffer strips in north-central Quebec, Canada, showed the annual mortality rate was 0.6% year^{-1} for white spruce, 0.4% year^{-1} for paper birch, 1.2% year^{-1} for black spruce (*Picea mariana* (Mill.)) and 2.2% year^{-1} for balsam fir (*Abies balsamea* (L.)) residual trees (Ruel et al. 2001, Ruel et al. 2003). In northern hardwood forests, single-tree selection resulted in an increase in mortality rate from 1.5% year^{-1} to 3.3% year^{-1} for a range of deciduous species (Caspersen 2006). I believe the greater mortality I observed compared to others may be related to two factors. (1) My study sites are located in a region with relatively low precipitation compared to previous studies, therefore the residual trees could already be stressed prior to harvest. (2) Variable retention harvesting creates more open conditions than some other partial-cut systems, such as shelterwood or single-tree selection, and would therefore be expected to produce a more stressful microclimate.

My observations of heavy crown dieback and mortality among the hardwood species provide insights into the different forms of mortality. I believe the majority of hardwood mortality in the VR sites was probably related to xylem dysfunction, from the abrupt increase in evaporative demand that occurs after partial harvesting (Bladon et al. In press). Additionally, the greater probability for more slender poplar (U and CD trees) and birch (U trees) residuals to suffer post-VR mortality supports the idea that increased wind exposure and bending may damage the xylem of tree stems, reducing hydraulic conductivity and intensifying moisture stress (Frederickson et al. 1994, Liu et al. 2003). This is potentially a greater problem for more slender stems due to much wider oscillations of the crowns than observed for trees with stout boles (Rudnicki et al. 2003).

Xylem dysfunction could potentially create leaf water deficits, stomatal closure, a decline in photosynthesis, loss of leaf area, and reduced tree growth, increasing the probability of whole-tree mortality (Kobe and Coates 1997). Generally, hardwood species are more susceptible to xylem dysfunction than conifers (Sperry and Sullivan 1992, Sperry et al. 1994, Maherali et al. 2004), which may explain why the heavy crown dieback and mortality was more predominant in these species. However, my results also support the notion that aspen may be more tolerant of this form of stress than many other hardwood species (Lieffers et al. 2001).

The majority of residual spruce mortality (80.0%) was due to windthrow. This was not surprising, as wind penetration in the stand increases after partial harvesting (Rudnicki et al. 2003, Bladon et al. In press), causing less efficient dissipation of turbulent energy by crown contact (Cremer et al. 1982, Savill 1983). Residual spruce trees were likely more susceptible to windthrow than the hardwoods for several reasons: 1) shallower rooting depths (Strong and La Roi 1983), 2) higher drag coefficients (Rudnicki et al. 2004, Vollsinger et al. 2005), and 3) greater stem mass than hardwoods (Meunier et al. 2002). Stem mass integrates several other variables, including stem diameter, tree height, wood density, stem taper, and crown canopy position, which together determine the critical turning moment required to break or uproot a tree (Achim et al. 2005).

I also observed greater windthrow of more dominant spruce trees, which is consistent with others (Lohmander and Helles 1987, Ruel 1989, Ruel et al. 2000), but is contrary to my expectation that trees with a high slenderness coefficient would be most susceptible to windthrow (Coates 1997, Meunier et al. 2002, Scott and Mitchell 2005). The higher vulnerability of more dominant spruce to windthrow may also be due to a greater stem mass than less dominant trees. Further, it has been noted elsewhere that there is a rapid increase in vulnerability to windthrow above a height of 10 – 12 m (Ruel 1995, Ruel et al. 2003), and the average height of the windthrown trees in the VR plots was 22.2 m. Additional studies of post-VR sites that focus on stand factors such as height, root systems, soil properties, age, root rot, crown length, pre-harvest stand density and/or slope position may help to determine the most important factors influencing windthrow risk in these sites.

The likelihood of spruce windthrow was greater for trees that were damaged during the harvesting. Additionally, the probability of windthrow increased as the percentage of the bole that was damaged increased. This suggests that the force of impact of the harvesting equipment, coupled with damage to structural roots, could potentially compromise tree stability and root anchorage, increasing the probability of windthrow. Further, wounds that expose the cambium or wood might promote additional tree death by increasing the susceptibility to fungal attack, causing stain, decay and reduced vigor (Franklin et al. 1987, Nichols et al. 1993, Seablom and Reed 2005).

If spruce residuals are not blown down after VR, it appears as though they will respond favorably to the increase in resource availability, with increased growth. The percentage increase in dbh from 2001 to 2005 for the surviving spruce was 2.6 to 3.8% higher than observed for aspen or birch, and was approximately the same as for poplar (Figure 2-4). This is consistent with many other observations of accelerated growth of spruce following release from competition for resources (Berry 1982, Yang 1991, Urban et al. 1994).

2.5 MANAGEMENT IMPLICATIONS

My results indicate that the mortality rate of hardwood species retained following VR harvesting could increase by as much as 4-times the natural mortality rate in the first several years following disturbance. If the primary objectives of VR harvesting are to provide critical habitat elements, ameliorate microclimate change, enhance connectivity for movement of organisms, or to sustain basic ecosystem functions (Franklin et al. 2002), then I recommend caution in applying VR, as high mortality rates could be a problem. Retention of more dominant aspen and birch, more stout poplar, or CD and U spruce residuals may achieve the objectives of providing a living legacy, as these trees appeared less susceptible to mortality. However, leaving many dispersed hardwood residuals may be a good strategy for rapid recruitment of snags. Conversely, large spruce trees, particularly those showing stem damage from the logging may provide immediate inputs of coarse woody debris, as these trees were most susceptible to windthrow. The increased wind speeds of VR cuts appears to be problematic, both for windthrow of the conifers and the stresses related to increased evaporative demand or xylem damage in the hardwoods. Therefore, managers should use strategies to reduce wind around residual trees. If living trees are an objective, leaving residuals in clusters, near stand edges or in sheltered landscape positions may reduce mortality. However, it may also be necessary to retain greater numbers of trees to ensure that the values of living, mature trees are sustained in regions where residual mortality could be high.

2.6 REFERENCES

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Table 2-1. Mean residual tree characteristics and standard errors by species from the mortality survey of variable retention (VR) harvested sites.

Species	Age (years)	Height (m)	htlc (m)	dbh (cm)	SC
Aspen	66.9 ± 1.86	21.9 ± 0.43	10.1 ± 0.56	36.2 ± 1.39	71.0 ± 1.98
Birch	73.0 ± 4.04	17.0 ± 0.59	3.47 ± 0.36	23.8 ± 1.22	79.6 ± 1.90
Poplar	66.8 ± 2.53	20.9 ± 0.54	4.02 ± 0.40	34.0 ± 1.47	69.1 ± 1.66
Spruce	53.3 ± 2.20	18.7 ± 0.63	2.43 ± 0.20	35.4 ± 1.38	54.6 ± 0.78

Abbreviations: htlc = height to live crown; dbh = diameter-at-breast-height; SC = slenderness coefficient.

Figure 2-1. Mean annual mortality rates and standard errors from natural and variable retention plots for white spruce, trembling aspen, paper birch, and balsam poplar.

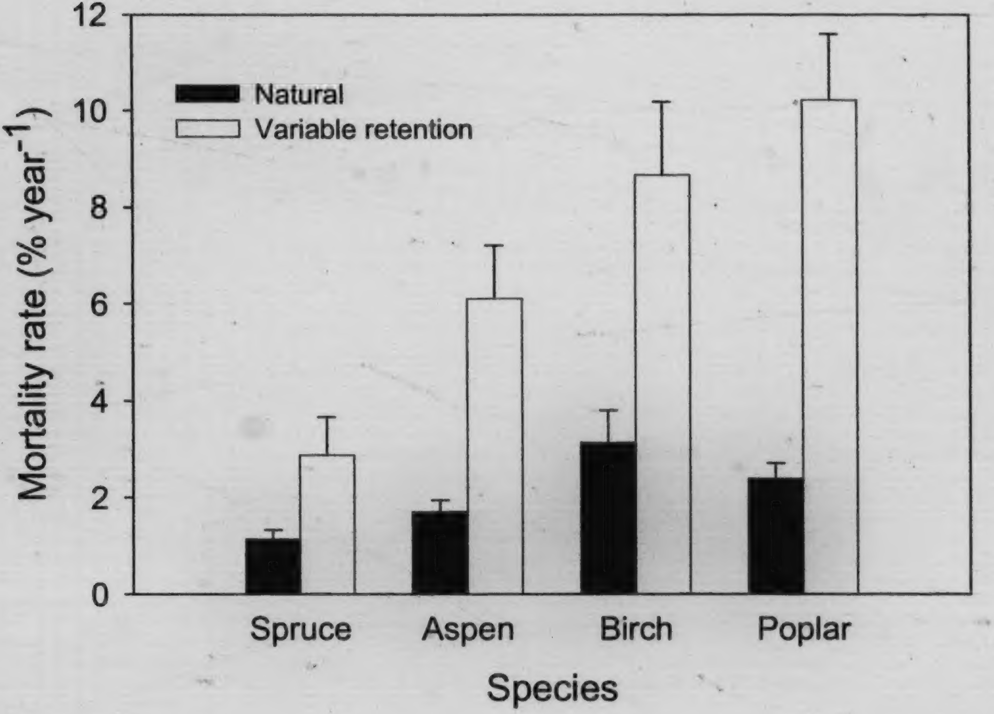


Figure 2-2. Residual tree health for white spruce, trembling aspen, paper birch, and balsam poplar 5 years after variable retention harvest.

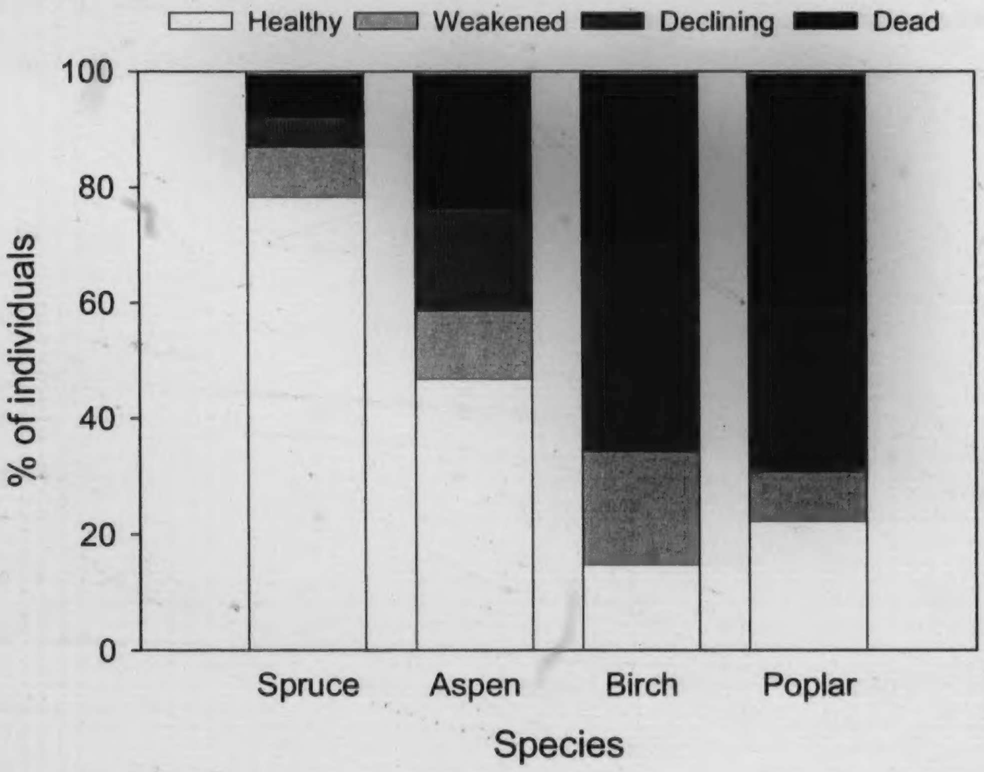


Figure 2-3. A comparison of the different forms of mortality for white spruce, trembling aspen, paper birch, and balsam poplar residuals 5 years after variable retention harvest.

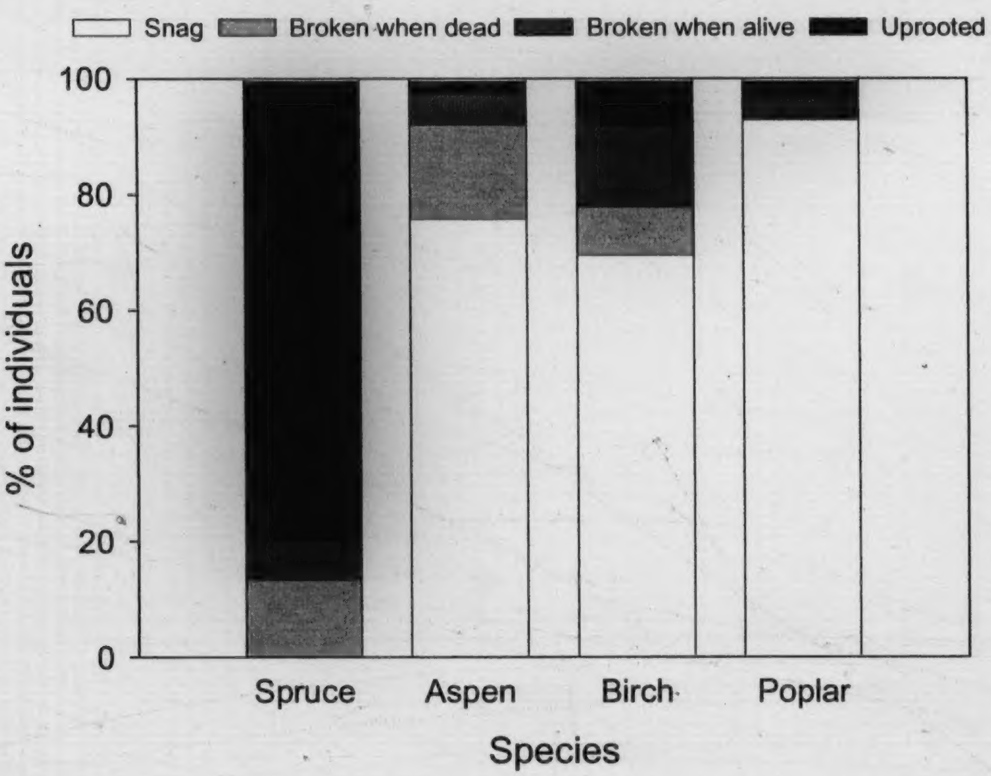
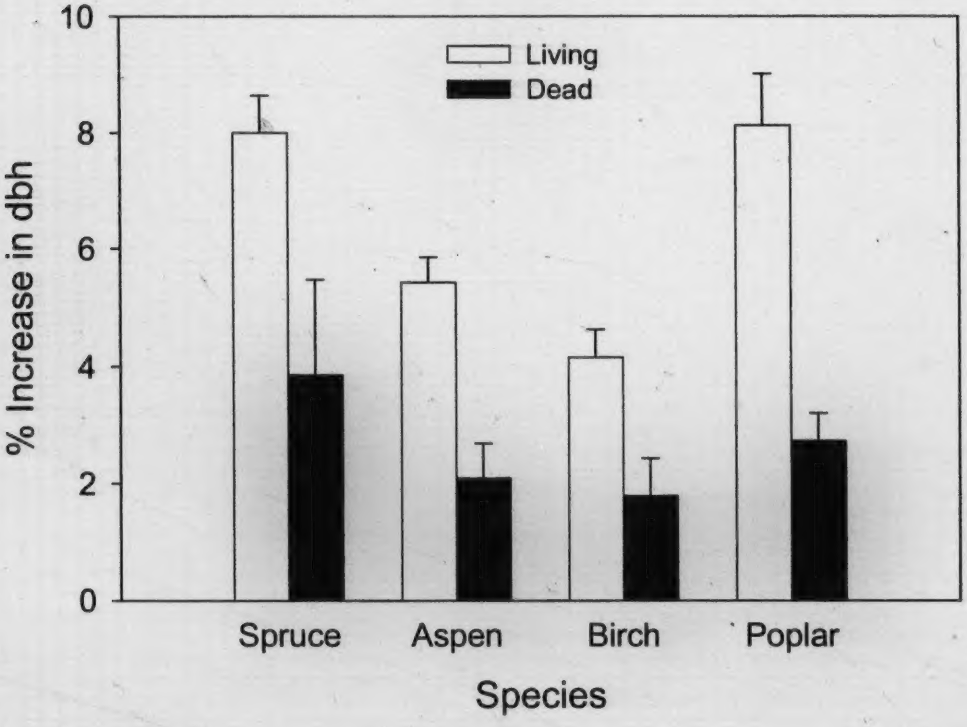


Figure 2-4. A comparison of the percentage (%) increase in diameter-at-breast-height (dbh) from 2001 – 2005 between living and dead residuals 5 years after variable retention harvest for white spruce, trembling aspen, paper birch, and balsam poplar.



Chapter 3

DIFFERENTIAL TRANSPIRATION BY THREE BOREAL TREE SPECIES IN RESPONSE TO INCREASED EVAPORATIVE DEMAND AFTER VARIABLE RETENTION HARVESTING[2]

3.1 INTRODUCTION

Variable retention (VR) and other partial-cut silvicultural treatments are being practiced over large parts of the world to address a broad array of forest management objectives (North et al. 1996, Progar et al. 1999, Zenner 2000, Sullivan et al. 2001). These practices leave single or small groups of trees in cutover areas. It is often assumed that residual trees will benefit from reduced competition and more open growing conditions (Wang et al. 1995, Liu et al. 2003). There are however, many examples where residual trees have not responded positively to these partial cutting treatments. There may be decreases in growth rates or higher rates of mortality for some years following VR harvesting (Roy et al. 2001, Bebber et al. 2005).

Apart from problems of increased probability of windthrow, VR may abruptly expose residual trees to altered microclimate, including increased fluctuations in wind speed (u), air temperature (T_a), relative humidity (RH), vapour pressure deficit (D) and net radiation (Q^*) (Cadenasso et al. 1997, Man and Lieffers 1999, Proe et al. 2001), producing greater evaporative demand in harvested areas (Zheng et al. 2000). While interactions can be complex, generally, evaporative demand is positively associated with T_a, D, u and Q^*; and is negatively associated with RH.

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[2] A version of this chapter has been published.
Bladon, K. D., U. Silins, S. M. Landhäusser, and V. J. Lieffers. 2006. Differential transpiration by three boreal tree species in response to increased evaporative demand after variable retention harvesting. Agricultural and Forest Meteorology.

The transpiration response of trees to greater evaporative demand has been shown to exhibit non-linear (asymptotic) relationships with individual components driving atmospheric moisture demand, such as increasing D or Q^* (Martin et al. 1997, Hogg et al. 2000, Ewers et al. 2002), or even a decline in transpiration at high D (Pataki et al. 2000). Both of these responses have been attributed to partial closure of stomata to maintain total water potential (Ψ) above a specific threshold, beyond which xylem dysfunction will occur (Hogg and Hurdle 1997, Bond and Kavanagh 1999). The narrowing of stomatal openings reduces stomatal conductance (g_s), and thus is associated with significant declines in photosynthetic rates (Dang et al. 1997, Hogg et al. 2000). If prolonged this may result in depletion of carbohydrate reserves, defensive compounds, and a loss of total leaf area (Waring 1987).

During prolonged periods of high atmospheric evaporative demand, some cavitation-induced embolism may be unavoidable in certain species, resulting in decreased water transport to foliage (Jones and Sutherland 1991, Sperry and Pockman 1993, Nardini and Salleo 2000). Xylem dysfunction leads to increased tension in the remaining conduits (Tyree and Sperry 1988), risking a runaway cycle of embolism (Tyree and Ewers 1991). Trees may approach this unstable embolism cycle, leading to catastrophic xylem dysfunction, after as little as 5 to 20% loss of sapwood hydraulic conductivity (K_Ψ) (Tyree and Sperry 1988). Trees experiencing such stress may suffer branch and root die-back, further limiting net carbon assimilation (Roy et al. 2001). A decline in photosynthesis will limit tree growth, which may increase the probability of whole-tree mortality (Kobe and Coates 1997). Therefore, I hypothesize that VR may produce microclimatic conditions that result in physiological stress, declining vigour and accelerated mortality of residual trees. To my knowledge, there have been no previous studies demonstrating the physiological response of various species of residual trees to the microclimatic change that occurs after VR harvesting.

This study examined the microclimate immediately after VR harvesting, and investigated the differential species responses in whole-tree water use to this change. The objective was to describe and compare tree sap flow and transpiration responses to microclimate change associated with VR for balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* (Moench) Voss) and paper birch (*Betula papyrifera* Marsh.), the typical retention species in boreal mixedwood stands. I hypothesized that after partial harvesting: (1) microclimate at the crown level would have lower RH and increased T_a, D, u and Q^*; (2) transpiration rates per unit leaf area (Q_l), mean daily maximum transpiration ($Q_{l\text{-}max}$) and mean total daily water use (Q_d) per tree would increase; and (3) that the hardwoods, poplar and birch, would have larger differences in Q_l and Q_d between VR trees and control trees, compared to spruce, because of their greater capability for water transport to their crowns (xylem hydraulic conductivity).

3.2 MATERIALS AND METHODS

3.2.1 Study Site Description

The study area was 40 km south-west of Drayton Valley, Alberta (53° 13′N, 114° 59′W) (approximately 900 m elevation) in the Lower Foothills Natural Subregion. The study area consisted of two sites approximately 300 m apart, within the e2 Low-bush cranberry ecosite (Beckingham et al. 1996). Topography was rolling with gentle slopes, and both sites had a very slight western aspect. Both stands were mixedwoods, consisting of trembling aspen (*Populus tremuloides* Michx.) (38.5%), paper birch (28.1%), balsam poplar (19.5%) and white spruce (13.9%). Prior to VR harvesting the overstory stand density was 1947.0 ± 289.4 trees ha^{-1}, mean basal area was 50.2 ± 9.6 m^{2} ha^{-1}, mean height was 15.8 ± 1.7 m and mean dbh was 16.9 ± 2.6 cm. The sites had a mesic moisture regime and a medium nutrient regime on a Grey Luvisol with a silty-clay texture developed over morainal till. The mean daily temperature is 2.3°C (-4.6°C – 9.1°C). The mean daily summer (June to August) temperature is 13.8°C (7.1°C – 20.5°C). The peak of summer photoperiod is approximately 17 hours day^{-1}. The mean annual precipitation is 535 mm, with ~77% falling as rain. The June to August precipitation is 260 mm.

3.2.2 Experimental design

The study design was approached similar to a "paired basin" watershed experiment, (before/after, control/treatment) allowing more powerful control to detect changes in microclimate than other sampling designs. The two sites had similar tree age, species composition, soil type, nutrient regime, moisture regime, slope and aspect. One site was to be harvested, with approximately 10% retention (VR site), and a second area was to remain as a closed canopy forest (control). The control was 100 m from the cut edge, while the site studied in the variable retention (VR) area was 100 m from the forest edge. In both the control and VR site, three co-dominant (CD) trees from each species were selected within a 30 m radius to accommodate the instrumentation. Only healthy trees, showing no sign of damage or disease were sampled. Therefore, due to heavy defoliation (~50.6% of the crowns) by large aspen tortrix (*Choristoneura conflictana* (Walker)) I was unable to sample the sap flux of trembling aspen in either site. Measurements of tree height, dbh (1.3 m) and live crown ratio were collected from each sample tree (Table 3-1).

The tree harvest was done by a feller buncher on July 9, 2003. During harvest, machines stayed at least 7 m from sample trees and skidders remained 15 m from the trees. This eliminated bole damage, and minimized soil compaction and root damage to the sample trees.

3.2.3 Micrometeorological measurements

Climate stations were established before harvest at the centre of both the control and treatment sites. All meteorological variables were continuously measured at a height of 12.1 m (mid-crown position) for a period of 26 days (June 13 – July 8) prior to the treatment (pre-harvest). The purpose of the pre-harvest measurements was to establish the pre-disturbance relation of the two sites to each other. Micrometeorological measurements continued for 32 days post-harvest (July 9 – 31 and August 13 – 21).

Air temperature (T_a) and relative humidity (RH) were measured with a Vaisala Temperature/ Humidity Probe (HMP35C, Campbell Scientific, Logan, UT, USA) protected by a multi-plate radiation shield. The data were used to calculate ambient vapour pressure (e_a; Pa), saturation vapour pressure (e_s; Pa) and vapour pressure deficit (D; Pa). Short wave radiation was measured with a Li-Cor 200SZ pyranometer sensor (Li-Cor, Lincoln, NE, USA), while net radiation (Q^*; W m^{-2}) data were collected with a net radiometer (NR-Lite and REBS Q-6, Campbell Scientific). An R.M. Young anemometer (Wind Monitor, 05103-10, Campbell Scientific) was used to determine wind speed (u; m s^{-1}) and wind direction. Two water content reflectometers (CS615, Campbell Scientific) were positioned in opposite directions, 15 m from the centrally located micrometeorological tower, and installed vertically in the upper 30 cm of soil at each site to provide volumetric water content (θ_v). Precipitation was measured with a universal precipitation gauge (5-780, Belfort Instrument). Meteorological variables were sampled every 5 seconds and averaged after 15 minutes using a CR10X control system (Campbell Scientific). The array was powered with a solar panel mounted on the tower with power storage in a 12 volt deep-cycle battery. All micrometeorological sensors were calibrated in the laboratory prior to installation in the field.

3.2.4 Potential evapotranspiration

Micrometeorological data were used with the Penman combination equation (Van Bavel 1966) to provide the potential evapotranspiration (ET_P; m s^{-1}) from each site:

Equation 3-1

$$ET_P = \frac{\Delta Q^* + \rho_a c_a u D}{\rho_\omega \lambda_\upsilon (\Delta + \gamma)}$$

where Δ is the slope of the saturation vapour pressure vs. temperature curve at the air temperature (Pa K^{-1}), Q^* is net radiation (J m^{-2} s^{-1}), ρ_a is the density of air (kg m^{-3}), c_a is the heat capacity of air (J kg^{-1} K^{-1}), u is wind speed (m s^{-1}), D is the vapour pressure deficit (Pa), ρ_ω is density of water (kg m^{-3}), λ_υ is latent heat of vaporization (J kg^{-1}), and γ is the psychrometric constant (Pa K^{-1}).

3.2.5 Sap flux measurements

Two constant-heat sap flow sensors constructed after Granier (1985, 1987) were installed at breast height on opposite sides of the stem, facing east and west, in each of the sample trees. For each sensor, two holes were drilled into sapwood with a vertical spacing of 10 cm. Each hole was drilled to a depth of 2.0 – 2.5 cm to ensure that the sensor was in contact with functional xylem. The mean sapwood depths of the sample trees (birch = 1.9 cm, poplar = 2.9 cm and spruce = 2.8 cm), indicated that the probes used (2 cm length) likely would have closely approximated the actual sap flux. If necessary for suitable installation, a chisel was used to remove a thin layer of the outer bark. A small amount (~0.5 mL) of hydrogen peroxide (30 mg mL^{-1} solution) was injected into each hole to destroy bacteria transmitted from the drill bit. Reflective foil was used to insulate the temperature field around the sensors, limiting the effects of solar radiation and convective heat loss.

The upper probe was heated constantly with a 0.2 W direct current, producing a maximum temperature difference of 8 – 10°C under zero flow conditions. The temperature differences, monitored with thermocouples, were related to the mass flow of water from the empirical calculation (Granier 1987):

Equation 3-2

$$v_s = 119 \times 10^{-6} \left(\frac{\Delta T_M - \Delta T}{\Delta T} \right)^{1.231}$$

where v_s (m s^{-1}) is the mean sap velocity on a sapwood area basis along a radius, ΔT_M is the temperature difference when sap flow is assumed to equal 0 (night values), and ΔT is the temperature difference between the two probes. As sap flow increases, progressively more heat is moved away from the upper probe, decreasing ΔT. A thermocouple multiplexer (AM25T, Campbell Scientific) was used to connect sensors to the data logger, where probe signals were scanned every 15-s and 15-min means were recorded. The rate of sap flow (Q, $m^3\ s^{-1}$) was then calculated as:

Equation 3-3 $$Q = v_s A_s$$

where A_s (m^2) is the cross-sectional sapwood area. This was determined for each tree from 1 cm disks cut at breast height (1.3 m) from frozen samples harvested at the end of the study. The sapwood-heartwood boundary was marked as samples thawed. Samples were scanned and A_s was calculated with imaging software (Sigma Scan 3.0, Jandel Scientific, San Rafael, CA, USA). The total Q for each tree was determined from the mean of the two probes in each tree. Total volumetric daily water use (Q_d; $m^3\ day^{-1}$) was calculated from the sum of all periods within a day.

Transpiration rate per unit leaf area (Q_l; $m^3\ H_2O\ m^{-2}\ A_L\ s^{-1}$) was calculated for each stem as follows (Ewers and Oren 2000):

Equation 3-4 $$Q_l = Q / A_L$$

where A_L (m^2) is the total leaf area for each tree (Table 3-1). I collected all leaves from each tree and oven-dried (65°C for 72 hours) in the laboratory. Leaves were then hand sorted to eliminate debris. The remaining leaves and petioles were weighed to determine the total dry biomass per plant (m_d; kg). The A_L for each tree was then calculated by:

Equation 3-5 $$A_L = m_d SLA$$

where *SLA* is the specific leaf area (i.e. one-sided leaf area per unit leaf dry mass; $m^2\ kg^{-1}$) from the sub-sample. Leaf sub-samples from the deciduous (approximately 100 leaves per tree) and coniferous trees (approximately 50 twigs with needles) were collected to capture the variability in leaf size and weight throughout the entire crown. Deciduous tree sub-sample leaf area was calculated using the average of three (3) measurements of all sub-sample leaves to reduce the potential error from a LI-3100 Area Meter (Li-Cor). Leaf areas of coniferous sub-samples were determined using a scanner and imaging software (Sigma Scan 3.0, Jandel Scientific).

3.2.6 Coupling calculations

The dimensionless decoupling coefficient ($0 \leq \Omega \leq 1$), where those trees that are aerodynamically well-coupled to the atmosphere have Ω near zero, was calculated for each tree species as (Jarvis and McNaughton 1986):

Equation 3-6 $$\Omega = \frac{(1+\varepsilon)}{(1+\varepsilon+g_a/g_c)}$$

where ε is Δ/γ, g_a is aerodynamic conductance and g_c is canopy conductance. Canopy conductance ($m\ s^{-1}$) was estimated as:

Equation 3-7 $$g_c = \frac{\gamma \lambda Q}{\rho_a C_p D}$$

where C_p is the specific heat of dry air at constant pressure ($J\ kg^{-1}\ K^{-1}$). Aerodynamic conductance ($m\ s^{-1}$) was calculated as:

Equation 3-8 $$g_a = \left[\frac{u}{u_*^{2}}\right]^{-1}$$

where u_* is the friction velocity (m s^{-1}), which was determined from:

Equation 3-9 $$u_* = \frac{\bar{u}\kappa}{\ln\left(z/z_o\right)}$$

where $\bar{u}$ is the mean wind speed (m s^{-1}), κ is von Karman's constant, z is the height of the wind measurement (m), and z_o is the roughness length (0.1 * tree height (m)).

3.2.7 Sapwood hydraulic characteristics

At the end of the field experiment, trees were destructively sampled. Stem sections 100 cm long and centred on breast height (1.3 m) were cut, double-wrapped in polyethylene bags (0.15 mm thick), iced and transported to the laboratory. The sections were kept water saturated and refrigerated (4°C) in a dark room for up to two weeks, until hydraulic conductivity was measured (Sperry et al. 1988, Mencuccini et al. 1997).

Stem samples (15 – 20 cm long), centred on the breast height position, were cut with a band saw. Cut surfaces were smoothed with a sharp, low-angle (30°) block plane, eliminating resinous exudates and sawdust from the surface (Mencuccini et al. 1997). Each stem segment was installed in an apparatus that used a hanging water column to generate a constant pressure head ($\Delta\Psi$) of 17.45 kPa across the sample, which was insufficient pressure to flush embolisms. Filtered (0.2 μm), degassed water was perfused through each sample in the natural direction of flow. Outflow water temperature was recorded to correct for variations in viscosity. An electronic balance and computer recorded outflow for 15 minutes following 5 minutes of stable flow.

Sapwood hydraulic properties were quantified as discussed in Reid et al. (2005). Hydraulic conductivity (K_Ψ, m^2 Pa^{-1} s^{-1}), as described by Darcy's law, was calculated using:

Equation 3-10 $$K_\Psi = \frac{QL}{A_s \Delta\Psi}$$

where Q is flow or volumetric discharge per unit time (m^3 s^{-1}) through the stem section with a sapwood area (A_s) and length (L). $\Delta\Psi$ is the water potential difference driving flow, expressed using pressure units (Pa). An estimate of the capacity of the stem segment to conduct water was calculated from:

Equation 3-11 $$Q_h = K_\Psi A_s$$

where Q_h (m^4 Pa^{-1} s^{-1}) is the hydraulic capacity, which expresses volumetric flow (m^3 s^{-1}) per unit of hydraulic gradient (Pa m^{-1}). This value provides a description of regulated flow through stems as the combined effects of hydraulic conductivity and conducting sapwood area under a unit hydraulic gradient. To quantify the relationship between the water conducting properties of xylem and leaf area, leaf specific hydraulic capacity (Q_L, m^2 Pa^{-1} s^{-1}) was defined as:

Equation 3-12 $$Q_L = Q_h / A_L$$

where A_L is the leaf area distal to the stem segment measured.

3.2.8 Total water potential measurements

On a warm, clear day in July 2005, sites were revisited to measure total water potential (Ψ) with a pressure chamber instrument (Model 600, PMS Instruments, Corvallis, OR, USA). Soil moisture was recharged by recent rains. Pressure chamber readings were taken at midday (1225-1625 MDT), when water stress would be highest. Sample twigs were collected from mid-canopy from trees that appeared healthy, with no signs of leaf senescence or branch dieback. I alternated between the control and VR site until 6 trees from each species at each site had been sampled.

3.2.9 Data analyses

Correlations of micrometeorological variables pre-harvest (June 13 – July 8) and post-harvest (July 9 – 31 and August 13 – 21) were compared between control and VR sites. Differences in slopes and intercepts were tested using *t*-tests in a method analogous to that of testing for differences between two population means (Zar 1999). Two-tailed *t*-tests were also used to compare Ψ between the control and VR site for each of species (PROC TTEST). Relationships between Q_l and D, Q^*, u and ET_P for all 3 species, in both the VR and control sites, were produced using hourly averages (0900 – 1500 MDT) from the entire post-harvest period. Days with precipitation were eliminated from the data set. The non-linear function $y = a(1\text{-}\exp(-kx))$ was used to fit curves to the relationships between individual species Q_l (y) and each of the micrometeorological variables (x) (PROC NLIN). Model parameters are presented in Table 3-2. An overall test for coincidental regressions was used to test whether the slopes and intercepts were identical (Zar 1999). Function parameters (k=slope and a=asymptote) were analysed using PROC

GLM and post-hoc mean separation tests (Tukey's) to determine where they were different between species and sites. Adjusted R^2 values for all equations were calculated as 1 – (error sum of squares / corrected total sum of squares) (Cornell and Berger 1987). All statistical analyses were performed using the SAS statistical package (Version 9.1, SAS Institute Inc., Carey, NC), with $\alpha = 0.05$ as the threshold for statistical significance.

3.3 RESULTS

3.3.1 Micrometeorology

Pre-harvest mean air temperature (T_a) was 13.9°C in both the control and treated sites. The post-harvest measurement period was warm, with mean T_a of 18.0°C in both the control and VR sites. The observed post-harvest T_a in the VR site was only 0.17°C (1.0%) lower than the predicted values determined from the pre-harvest calibration period. While there was a slight difference in T_a between the two sites from the pre-harvest to the post-harvest period, there was no difference in the slopes ($t = 0.97$; $P > 0.30$) or intercepts ($t = -0.49$; $P > 0.50$) of the bivariate plot of the control vs. VR site before and after treatment (Figure 3-1A).

Mean relative humidity (*RH*) declined 9%, from 0.66 to 0.60, in the control site from the pre- to post-harvest period, while decreasing 14%, from 0.76 to 0.65, in the VR site. The bivariate plot of *RH* of the control vs. VR site (Figure 3-1B) showed a slightly lower intercept and greater slope, or drier atmosphere, in both sites post-harvest. The slopes ($P < 0.001$) and intercepts ($P < 0.001$) were significantly different. However, the actual difference between the observed and predicted *RH* in the VR site, post-harvest was only 0.018 (3.6%).

Mean vapour pressure deficit (*D*) in the control site increased 44% from the pre-harvest ($\bar{X}$ = 707.4 Pa) to the post-harvest measurement period ($\bar{X}$ = 1023.3 Pa). Similarly, in the VR site, mean *D* increased 53% from the pre-harvest ($\bar{X}$ = 617.7 Pa) to the post-harvest period ($\bar{X}$ = 950.1 Pa). The slopes ($P < 0.001$) and intercepts ($P < 0.001$) of the plot of *D* between the control and VR site were different from the pre- to post-harvest period (Figure 3-1C). However, the observed post-harvest *D* in the VR site was only 18.8 Pa (2.7%) different from the predicted values.

Wind speed (*u*) in the VR site increased by several fold after harvesting. The mean *u* observed prior to harvest in the control site was 0.25 m s^{-1} (0 – 1.40 m s^{-1}) and in the VR site was 0.13 m s^{-1} (0 – 0.67 m s^{-1}). The post-harvest mean *u* declined to 0.14 m s^{-1} (0 – 1.01 m s^{-1}) in the control site, while increasing in the VR site to 0.50 m s^{-1} (0 – 3.57 m s^{-1}). This equates to a mean decrease in *u* of 44% in the control site and a 284% increase in the VR site after harvesting. Both the slope and intercept of the bivariate plot of *u* of the control vs. VR site shifted upwards (Figure 3-1D), reflecting the large increase in *u* in the VR site post-harvest (slopes: $P < 0.001$; intercepts: $P < 0.001$). The actual difference between the observed and predicted *u* in the VR site, post-harvest was 0.28 m s^{-1} (339.6%).

Both the pre-harvest and post-harvest periods had mostly sunny days. Before the harvest mean net radiation (Q^*) during the midday (11:00 – 14:45), when peak daily Q_l was observed, was 363.9 W m^{-2} (33.7 – 659.5 W m^{-2}) in the control and 224.9 W m^{-2} (24.0 – 545.1 W m^{-2}) in the VR site. The post-harvest mean midday Q^* was 469.6 W m^{-2}

(72.2 – 653.9 W m^{-2}) in the control and 367.8 W m^{-2} (110.3 – 632.7 W m^{-2}) in the VR site. This represents a mean increase in Q^* of 29% in the control and 63% in the VR site. There was a significant difference in the pre- and post-harvest slopes ($P < 0.001$) and intercepts ($P < 0.001$) of the bivariate plots of Q^* between the control and VR site (Figure 3-1E). The observed post-harvest Q^* in the VR site was 79.9 W m^{-2} (52.5%) greater than the predicted values determined from the pre-harvest calibration period.

Prior to harvest, volumetric soil moisture (θ_v) in the control and VR sites tracked each other through precipitation events (Figure 3-2). The control site had higher θ_v ($\bar{X}$ = 0.359) compared to the VR site ($\bar{X}$ = 0.335) prior to harvest. After harvest, the VR site θ_v ($\bar{X}$ = 0.402) rose above the control ($\bar{X}$ = 0.332). The full range of θ_v values in both the control and VR site were within the typical range of plant available water or gravitational water values for a silty-clay soil (Dingman 2002). In days following precipitation, θ_v declined more rapidly in the control site than the VR site. Total precipitation pre-harvest was normal with 72.8 mm, but was well below average during the post-harvest period with just 43.4 mm of precipitation.

Throughout the measurement period before the harvest, potential evapotranspiration (ET_P) traces in the control site were slightly greater than observed in the VR site (Figure 3-3A). Immediately following harvest, this trend was reversed, with ET_P values in the VR site exceeding those in the control site (Figure 3-3B). While control ET_P values decreased minimally, the values in the VR site were doubled and often tripled following the harvest. A mean daily sum of 15 min. ET_P values showed a 9% decline in the control site from 2.05 mm d^{-1} (pre-harvest) to 1.86 mm d^{-1} (post-harvest). Conversely, there was a 290% increase mean daily ET_P in the VR site from 1.27 mm d^{-1} (pre-harvest) to 4.95 mm d^{-1} (post-harvest). In the control site the average number of hours per day when ET_P was greater than 0 increased from 14.4 hrs d^{-1} (pre-harvest) to 14.6 hrs d^{-1} (post-harvest), compared to the increase from 13.8 hrs d^{-1} (pre-harvest) to 17.5 hrs d^{-1} (post-harvest) in the VR site.

3.3.2 Transpiration rates

Post-harvest daily patterns of transpiration rates per unit leaf area per tree (Q_l) illustrate that transpiration in white spruce was generally lowest among the species (Figure 3-4 A-C). Spruce also showed the greatest differences between the control and VR sites; midday Q_l was 2 times greater in VR site trees compared to the control site. Alternatively, paper birch had higher Q_l than spruce, but showed moderate differences between sites, with Q_l in the VR site 1.25 – 1.5 times greater than in the control site. Balsam poplar generally showed similar Q_l as birch post-harvest; however, there were only marginal differences in the diurnal patterns of Q_l in the control and VR site (Figure 3-4C). The timing of water use also appears to be different between the control and VR site, with Q_l beginning earlier in the day and extending later into the evening and even into the pre-dawn hours in the VR site.

The $Q_{l\text{-}max}$ was about 2.5-times greater in spruce trees in the VR site than in the control during the post-harvest period (Figure 3-5A). Similarly, birch trees in the VR site had a $Q_{l\text{-}max}$ approximately 1.6-times greater than in the control site. Balsam poplar trees $Q_{l\text{-}max}$ was only marginally different between the two sites. Variation in total daily transpiration (Q_d) among species and treatments showed a similar pattern as $Q_{l\text{-}max}$. Spruce trees showed the greatest difference in Q_d per tree, with VR site trees utilizing approximately 3.2-times more water per day than control trees (Figure 3-5B). Total daily transpiration for birch was about 1.6-times greater in the VR site than in the control throughout the post-harvest measurement period, while only a marginal difference in Q_d was evident for poplar trees. The maximum Q_d values occurred on days which were characterized by high T_a, D and Q^*, low RH and above average midday u.

Differential responses among species to individual microclimate variables were also evident between the VR and control sites. Asymptotic relationships between daytime Q_l and D, Q^*, u and ET_P were observed for all 3 species in both sites (Figure 3-6). All species had increased Q_l with D but, spruce was least responsive and poplar was most responsive to changes in D in both sites. Additionally, there were strong differences between the VR and control sites in the relationship between Q_l and D for spruce ($P < 0.0001$), while weaker, yet significant differences (particularly at low D) were observed in birch trees ($P < 0.0001$) between the two sites. No differences in the relationships were evident for poplar ($P = 0.39$) between VR and control sites. I observed similar general patterns for Q_l in relation to Q^* in both sites (i.e. spruce < birch < poplar) but, the relationships between Q_l and Q^* were significantly different ($P < 0.0001$) between the VR and control site for all 3 species (Figure 3-6). The pattern of Q_l across the range of u values among species was generally similar to the response to D and Q^* (i.e. spruce < birch < poplar). However, at low wind speeds, Q_l of all 3 species appeared to be greater in the control trees compared to the VR trees. Furthermore, at the higher u observed in the VR site, spruce Q_l continued to rise at a similar rate as observed in the control site ($P = 0.12$). Conversely, poplar Q_l increased at a much lower rate in the VR site with increased u ($P < 0.0001$). Despite the greater u in the VR site, the highest Q_l values observed in the VR trees rarely exceeded those observed in the control site for this species. The response of birch to increased u in the VR site was intermediate to the other two species. Transpiration increased with greater u, but at a slightly slower rate than in the control site ($P < 0.001$). The combined effect of these three microclimatic variables is reflected in evaporative demand. The general pattern of species sensitivity and differences in Q_l between VR and control sites for ET_P was most similar to the patterns observed in the response to wind speed. In spruce, Q_l was similar in the VR and control sites at low ET_P. However, the increase in Q_l with high ET_P was greater in the VR site compared to the control site for this species ($P < 0.0001$). In contrast, at low evaporative demand, poplar transpiration was notably lower and the rate of increase in Q_l with ET_P was not as steep in the VR site as in the control site ($P < 0.0001$). At high evaporative demand, the increase in poplar Q_l in the VR site was limited compared to the other two species. For birch, the overall response in Q_l to ET_P was similar in both sites ($P = 0.26$), and intermediate between the responses observed in spruce and poplar.

Mean separations tests of the non-linear function parameters for the relationships between transpiration and the micrometeorological variables indicated that the asymptotes (a) were different between all species and between the control and VR sites (Table 3-2). However, tests of slopes (k) showed no differences between any of the three species, but still showed differences between the two sites.

3.3.3 Decoupling coefficients

The mean decoupling coefficients (Ω) in the control site indicated that white spruce was the most well coupled species to the atmosphere ($\Omega = 0.16$), followed by paper birch ($\Omega = 0.36$), and balsam poplar ($\Omega = 0.40$). Although the decoupling coefficients of all species were lowered in the VR sites (indicating greater atmospheric coupling), spruce experienced the lowest relative change in atmospheric coupling ($\Omega = 0.11$, 33% increase), followed by birch ($\Omega = 0.19$, 47% increase) and poplar ($\Omega = 0.18$, 55% increase).

3.3.4 Hydraulic characteristics

Main stem K_{Ψ}, Q_h and Q_L was generally greater in the VR site than the control site for all 3 species (Figure 3-7). None of the differences were statistically significant for any of the species. However, there were consistent differences between the species in their ability to transport water to their leaves. For all of the hydraulic characteristics I found paper birch > balsam poplar > white spruce in both the control and VR site. The small sample size (n = 3) may have contributed to the lack of significant difference in hydraulic characteristics between VR and control trees.

3.3.5 Total water potential

Variable retention harvesting resulted in significantly lower midday Ψ in the VR trees than in the control trees for all 3 species (Figure 3-8). The mean Ψ were significantly more negative in the VR trees than in the control trees for paper birch ($P = 0.02$), balsam poplar ($P = 0.04$), and white spruce ($P = 0.01$).

3.4. DISCUSSION

3.4.1 Micrometeorology

Variable retention (VR) harvesting produced a nearly three-fold increase in potential evapotranspiration (ET_P) immediately following harvesting. The most dramatic change in meteorological variables contributing to the increase in evaporative demand was the large increase in wind speed (u) at crown level in the VR site. Rudnicki et al. (2003) observed similar magnitudes of u increases (3-times) at the canopy level following thinning of lodgepole pine stands. As u increases, leaf boundary layer resistance decreases, directly influencing transpiration rates, photosynthetic rates, and leaf temperature (Daudet et al. 1999, Wullschleger et al. 2000). Depending on how well coupled a plant is with the atmosphere, increased flow of air over a leaf should increase turbulence, boundary layer conductance and, hence increase transpiration rates (Van Gardingen and Grace 1991, Hollinger et al. 1994).

The 63% increase in midday net radiation (Q^*) in the VR site also contributed to the near tripling of ET_P. Exposure of residual trees to increased radiant energy could partially explain the increased transpiration rates per unit leaf area (Q_l) and more negative total water potentials (Ψ) measured in all three species in the VR site. Increases in Q^*, and its influence on leaf temperature, has been observed to increase stomatal conductance (g_s) and Q_l in many species (Wullschleger et al. 2000, Pataki and Oren 2003). While I do not have data on leaf temperatures, I speculate that during very calm conditions leaf temperature increased as more of the crowns were fully exposed to solar radiation. This may have had a greater influence on transpiration rates of white spruce compared to the deciduous species because of the long, dense crowns of the conifers.

Contrary to my hypotheses, I did not observe large decreases in relative humidity (*RH*) or increases in air temperature (T_a) and vapour pressure deficit (D) at the crown level in the VR site. While the change in these variables following harvesting may have been statistically significant because of a very large sample size (> 2500 measurements), the actual differences appear to be physiologically negligible. In contrast, others have demonstrated that at positions near ground level (~0.2 m) harvested stands had lower *RH* and higher T_a and D than control sites (Barg and Edmonds 1999, Man and Lieffers 1999, Zheng et al. 2000). The discrepancy between these results and my findings is likely related to strong differences in advection and lapse conditions for water vapour and sensible heat at mid-canopy (12 m) of my sites, producing very similar humidity and temperature conditions between control and VR sites (Oke 1987).

I also observed considerable increases in volumetric soil moisture (θ_v) in the partial cutover, despite below average precipitation during the post-harvest period. Decreased total transpiration and rainfall interception following harvesting is probably responsible for increased θ_v in the VR site, similar to other studies (Childs and Flint 1987, Kranabetter and Coates 2004). Also, given the fine soil texture at my sites, it is likely that xylem dysfunction would provide a greater limitation to plant flux than rhizosphere conductance (Sperry et al. 1998). Thus, any differences in Q_l observed in my study were unlikely to be related to θ_v.

3.4.2 Tree response

Contrary to my hypothesis, that all species would respond to greater ET_P in the VR site with increased water use, maximum transpiration per unit leaf area ($Q_{l\text{-}max}$) and total daily water use (Q_d) for balsam poplar trees in the VR site was only marginally greater than in the control trees. Relative to paper birch and white spruce, the poplar trees had high $Q_{l\text{-}max}$ and low mean total water potential (Ψ) in the control site. Additionally, the saturation of Q_l at high D and Q^* (Figure 3-6) by this species in the control site suggests stomatal closure to maintain Ψ above the critical point of xylem cavitation. These findings provide evidence that poplar, with its steep increase in Q_l with D or Q^*, may normally function with a minimal safety margin against catastrophic xylem dysfunction (Tyree et al. 1994), compared to the low level for saturation of spruce. It must also be remembered, however, that apparent difference in the way that Q_l responded to D between the control and VR sites (Figure 3-6) was related to other values such as u or Q^*, which actually varied between the two sites. While mid-day Ψ for poplar in my study was as low as -2.1 MPa, total water potentials of -1.5 MPa in balsam poplar and other cottonwoods have been observed to result in as much as 50% loss of hydraulic conductivity from cavitation (Sperry et al. 1994). Thus, poplar trees in the VR site likely responded to the abrupt increases in u and ET_P with further stomatal closure, in order to limit Q_l and $Q_{l\text{-}max}$ to prevent runaway cavitation (Schulte et al. 1987, Hinckley et al. 1994, Rood et al. 2003). However, response curves for this species (Figure 3-6) show that at low ET_P, transpiration in the VR site trees was lower than Q_l of the control trees, indicating that the VR trees may have suffered some xylem dysfunction. Shortly after the VR harvest, I also noted leaf rolling and leaf wilting in the poplar trees. By the summer of

2005, many of the poplar residuals in the VR site had shed leaves from their upper canopy, and several nearby trees had died. Shedding leaves and small twigs is a common drought response of cottonwood species (Rood et al. 2000), and is considered to be a mechanism to reduce transpirational water loss after xylem cavitation (Zimmermann 1978).

My laboratory measurements of hydraulic conductivity and other hydraulic characteristics indicate that VR harvesting did not result in significant reductions in the ability of the main stems of poplar to transport water to their leaves. Part of the reason for this lack of significance might be related to the small sample size (n = 7). However, xylem dysfunction typically occurs in the most distal and expendable branches (i.e. vulnerability segmentation) rather than the main bole (Tyree and Sperry 1989, Tyree et al. 1993), so the lack of difference in hydraulic characteristics between the two sites is not surprising. My observation of upper crown dieback and subsequent development of adventitious branches on the stems of balsam poplar in partial cut areas are consistent with the theory of vulnerability segmentation.

My data for $Q_{c\,max}$ and Q_c indicates that white spruce responded well to the VR harvest. The nearly 3-fold increase in $Q_{c\,max}$ and Q_c of spruce in the VR site over the control site trees suggests that this species was able to respond directly to the rise in ET_0, with only limited stomatal closure. White spruce Q_c was positively related to both D and Q^*, but the response curves show that Q_c was still able to increase with greater D and ET_0 in the VR site (Figure 3-6). The substantial increase in $Q_{c\,max}$ in the spruce trees is likely to have contributed to the more negative midday Ψ values I observed for this species in the VR site. However, there was probably limited risk of cavitation because (1) the sap fluxes were comparatively low, and (2) like many coniferous species, spruce are highly resistant to water stress-induced cavitation (Sperry et al. 1994, Maherali et al. 2004). The ability of spruce to increase Q_l, $Q_{l\text{-}max}$ and Q_d in response to increased ET_P could translate into increased carbon fixation and growth, as observed in other coniferous species following partial harvesting (Bebber et al. 2003).

Paper birch residual trees also had greater Q_l in response to increased ET_P in the VR site. Similar to spruce, the Q_l response curves for birch (Figure 3-6) indicate that trees in the VR site were able to increase Q_l at high wind speeds. Furthermore, at high D and Q^*, trees in the VR site transpired at higher rates than trees in the control sites. However, there appears to be some limitation on water use by birch in the VR site. At low evaporative demand, Q_l in VR site trees rose more slowly than in the control trees, suggesting either stomatal closure or xylem dysfunction. Additionally, the mean $Q_{l\text{-}max}$ was only about 1.6-times greater for VR trees than control trees for this species, while ET_P increased nearly 3-fold. Like many other deciduous species, birch trees are known to be extremely susceptible to water stress-induced cavitation (Sperry and Sullivan 1992). Thus, some stomatal closure in the VR site trees likely occurred in response to increased u and ET_P in order to prevent Ψ values from dropping to levels inducing extensive cavitation. However, the general increase in Q_l with greater evaporative demand supports the hypothesis that stomata of *Betula* trees are incapable of long-term regulation of Q_l below levels inducing cavitation (Sperry and Pockman 1993). The highly negative Ψ values measured in birch trees in the VR site provides additional evidence of water stress sufficient to produce considerable cavitation and embolism (Sperry et al. 1994). If high ET_P persists for several years after VR, xylem dysfunction in birch could be cumulative and dieback may appear in subsequent years. It is important to consider that birch has been reported to have the ability to refill embolized xylem tissue (Sperry et al. 1994). Thus, if refilling is a viable mechanism to help this species cope with atmospheric drought-induced cavitation, then constraining Q_l through stomatal closure may not be as important for birch as for poplar. Refilling of embolized conduits could allow residual birch trees to delay crown dieback by re-increasing hydraulic conductivity. However, the potential root damage or soil compaction associated with normal harvesting operations (Kozlowski 1999) could prevent this species from using this mechanism to cope with the stresses associated with large and persistent increases in ET_P in VR harvested stands. Thus, I believe that the inability to control Q_l in response to high evaporative demand combined with the potential inability to repair xylem dysfunction due to root damage could explain the signs of leaf rolling, wilting, crown dieback and whole-tree mortality of birch residuals that I have observed in partially harvested cutovers throughout the region.

Estimates of the degree of canopy-atmosphere coupling indicated that balsam poplar were the least coupled species ($\Omega = 0.40$), likely because they had the thickest leaf boundary layer of the three species due to their large and smooth leaves. However, I found this species to be highly coupled in the VR site ($\Omega = 0.18$). My findings in the control site were similar to Hinckley et al. (1994), who found *Populus* hybrid trees to be partially decoupled from the atmosphere ($\Omega = 0.66$). As a result of moderate coupling, poplar transpiration would be highly dependent on Q^* and on the factors that influence canopy boundary layer, such as u and canopy roughness, rather than D (Jarvis and McNaughton 1986). Similarly, paper birch, was moderately coupled in the control site ($\Omega = 0.36$), and was highly coupled in the VR site ($\Omega = 0.19$). I did not anticipate that birch would have similar Ω values as poplar; however, the ability of the leaves of both species to swing in the wind likely reduces the boundary layer resistance comparably. Alternatively, white spruce was found to be highly coupled to the atmosphere in both the control ($\Omega = 0.16$) and VR site ($\Omega = 0.11$). Similar to other conifers, spruce possibly had high atmospheric coupling because of their many, small leaves, aerodynamically rough canopy and large boundary layer conductance (Meinzer 1993, Martin et al. 1999). While some conifers have been shown to be poorly coupled due to high needle packing of sun shoots (Smith and Carter 1988), this was likely not the case for the sample trees which were recently exposed from closed canopy conditions. I believe that the large and persistent increase in u, combined with the overall increase in canopy surface roughness and atmospheric turbulence following VR harvesting, greatly increased the canopy-atmosphere coupling in all species. As u increased in the VR site, the leaf boundary layer was likely eroded in all species, increasing aerodynamic conductance (g_a) and stomatal control of Q_l (Schuepp 1993, Martin et al. 1999, Wullschleger et al. 2000). This suggests that when there are large and persistent increases in u, as in VR cutovers, Q_l will be primarily driven by the vapour pressure gradient between the leaf surface and the surrounding air, and relatively insensitive to changes in Q^* (Hollinger et al. 1994). This is consistent with suggestions by Wullschleger et al. (2000) that tree response to changes in u, Q^* and D are highly dynamic and related to forest structure.

Immediately after VR harvesting, I observed increased ET_P and various signs of stress in balsam poplar and paper birch residual trees. Long-term stomatal regulation of Q_l to prevent xylem cavitation is unlikely for both hardwood species. Thus, poplar and birch residual trees may suffer extensive dieback and mortality, unless they are capable of adapting within a couple years after harvesting. I believe that only those trees with sufficient root or twig xylem conductivity, to meet the greater evaporative demand, will respond favourably to VR harvesting. Additional research is necessary to determine if it is possible to identify trees at the time of harvest that are most likely to adapt well to the abrupt change in microclimate. For white spruce, I feel that, as long as they are windfirm, most trees should benefit from reduced competition and more open growing conditions after partial harvesting.

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Table 3-1. Mean sample tree characteristics by species (Bw = paper birch; Pb = balsam poplar; Sw = white spruce) and standard errors of the mean from the control (CT) and variable retention (VR) sites (n = 3).

Species-Site	dbh (cm)	TH (m)	A_L (m^2)	A_s (cm^2)	Age (yrs)	LCR
Bw-CT	14.6 ± 0.7	12.7 ± 0.56	25.6 ± 6.1	105.7 ± 20.5	48.0 ± 2.9	63.3 ± 1.7
Pb-CT	19.6 ± 1.5	16.3 ± 0.58	30.0 ± 4.9	163.4 ± 21.7	50.0 ± 2.8	55.0 ± 8.7
Sw-CT	18.7 ± 3.2	16.3 ± 2.3	27.6 ± 2.7	86.8 ± 7.5	45.8 ± 4.9	88.3 ± 1.7
Bw-VR	14.6 ± 1.8	12.7 ± 1.4	23.8 ± 6.0	95.1 ± 21.3	47.1 ± 1.7	66.7 ± 4.4
Pb-VR	16.7 ± 0.1	15.2 ± 0.3	18.7 ± 2.8	100.9 ± 15.4	51.7 ± 3.9	35.0 ± 5.8
Sw-VR	16.0 ± 1.8	14.6 ± 1.5	33.8 ± 9.9	121.6 ± 32.8	30.8 ± 0.9	91.7 ± 1.7

Abbreviations: dbh = diameter at breast height; TH = total height; A_L = leaf area; A_s = sapwood area; LCR = Live crown ratio.

Table 5.2. Estimates of model parameters and standard errors of the means (s_x) for the non-linear model ($y = a(1-\exp(-bx))$) used to fit curves to the relationships between species transpiration rates per unit leaf area (J_l) and the micrometeorological variables. The dependent variables in the model were paper birch (Bw), balsam poplar (Pb) and white spruce (Sw) J_l from the clearcut (CT) and variable retention (VR) sites. The independent variables in the model were vapour pressure deficit (D), net radiation (Q^*), wind speed (u) and potential evapotranspiration (ET_0).

Species	Treatment	Independent variable	a	s_a	b	s_b	r^2
Bw	CT	D	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Q^*	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		u	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		ET_0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	VR	D	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Q^*	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		u	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		ET_0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Pb	CT	D	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Q^*	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		u	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		ET_0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	VR	D	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Q^*	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		u	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		ET_0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Sw	CT	D	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Q^*	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		u	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		ET_0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	VR	D	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Q^*	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		u	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		ET_0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Figure 3-1. Relationships between control and variable retention site micrometeorological variables, pre-harvest (triangles) and post-harvest (crosses), for A) air temperature (T_a; pre-harvest y = 1.0484x – 0.7031; post-harvest y = 1.0425x - 0.7687), B) relative humidity (*RH*; pre-harvest y = 1.007x + 0.0576; post-harvest y = 1.0219x + 0.0302), C) vapour pressure deficit (*D*; pre-harvest y = 0.9926x - 0.0844; post-harvest y = 1.0067x - 0.0802), D) wind speed (*u*; pre-harvest y = 0.4668x + 0.0074; post-harvest y = 2.0119x + 0.1872) and E) mean midday (1100 – 1445 MDT) net radiation (Q^*; pre-harvest y = 0.679x – 30.881; post-harvest y = 0.5654x + 102.3). Best fit lines not shown for clarity.

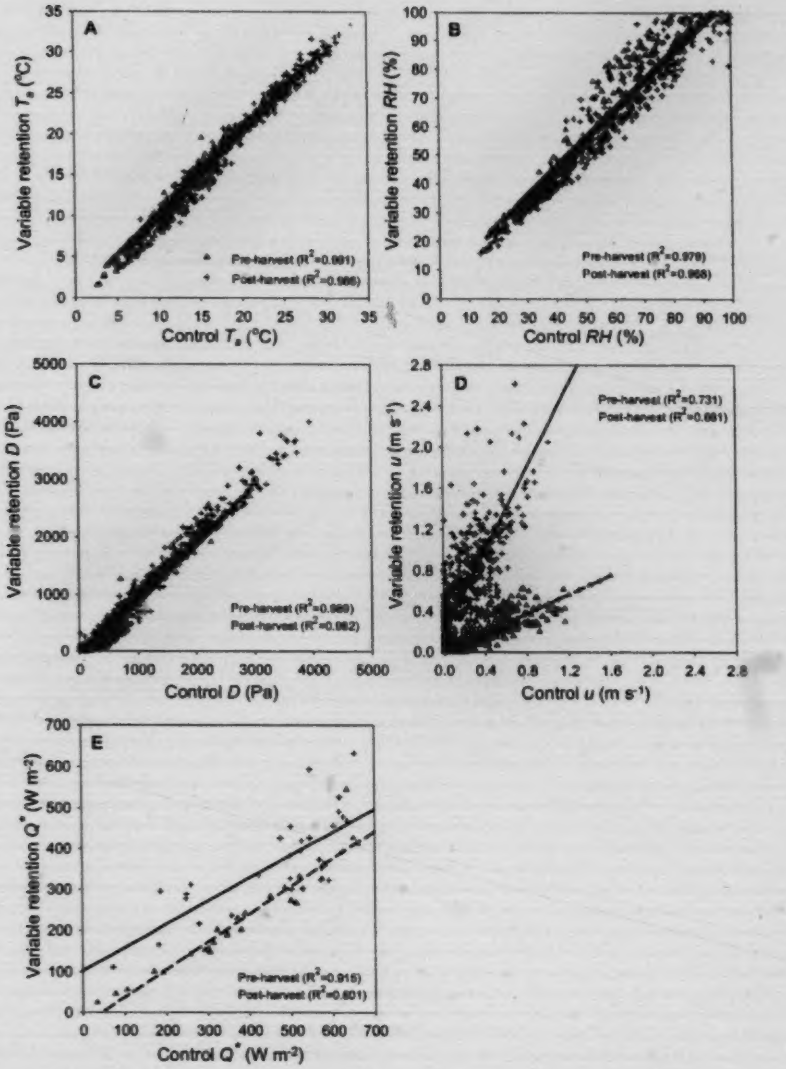


Figure 3-2. Mean daily volumetric soil moisture content (θ_v) and precipitation (mm) in the control and variable retention sites for each day pre- and post-harvest (June 13 – July 31 & August 13 – 21, 2003). The arrow indicates the time of partial harvest (July 9, 2003).

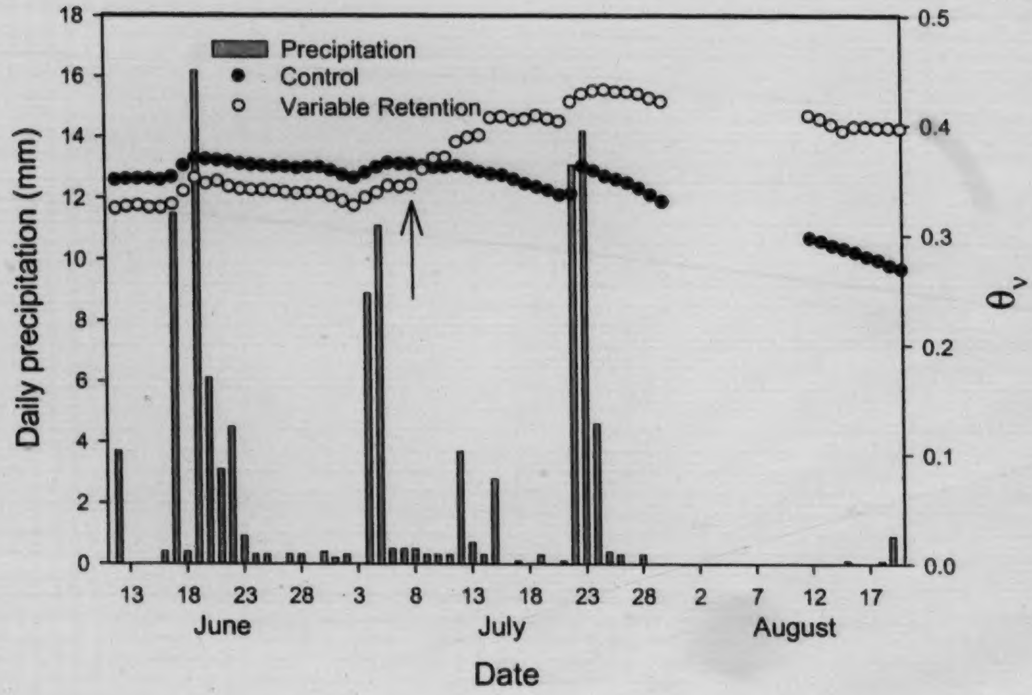


Figure 3-3. Typical 3-day pattern of potential evapotranspiration (ET_P) in the control and variable retention sites, determined from the Penman combination equation for free-water evaporation. A) Pre-harvest (July 6 – 8, 2003) and B) Post-harvest (July 15 – 17, 2003).

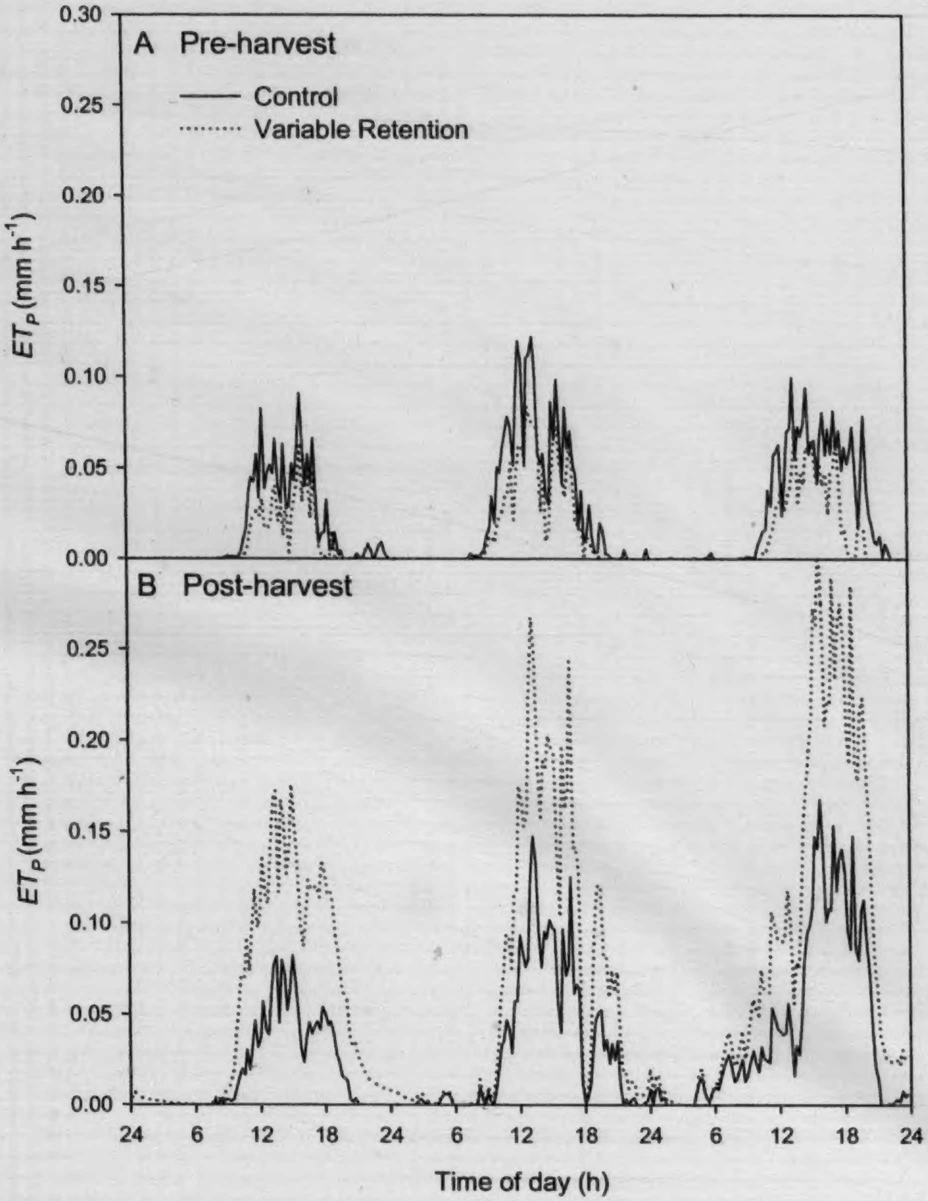


Figure 3-4. Typical pattern of mean transpiration rate per unit leaf area per tree (Q_l) on 3 clear days following partial harvest. A) white spruce, B) paper birch and C) balsam poplar from the control (solid line) and variable retention (dashed line) sites (July 15 – 17, 2003).

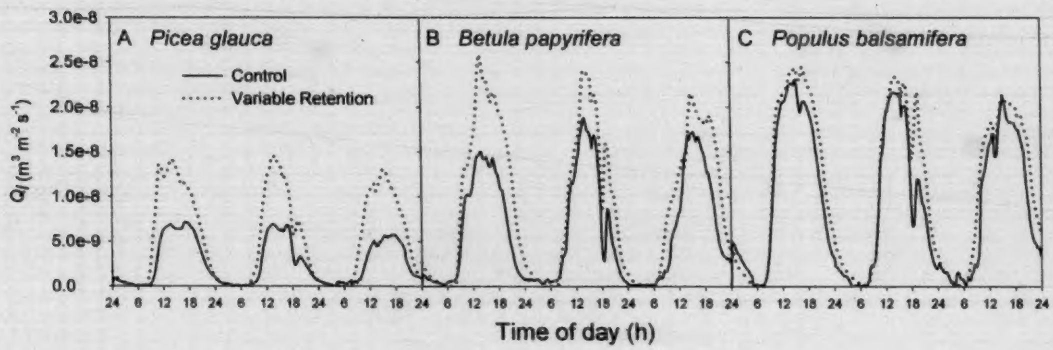


Figure 3-5. A) Mean daily maximum transpiration rate per unit leaf area (Q_{l-max}) and B) mean daily water use (Q_d) per tree of white spruce, paper birch, and balsam poplar from the control and variable retention sites for the entire post-harvest period (July 9 – 31 and August 13 – 21, 2003; n=3).

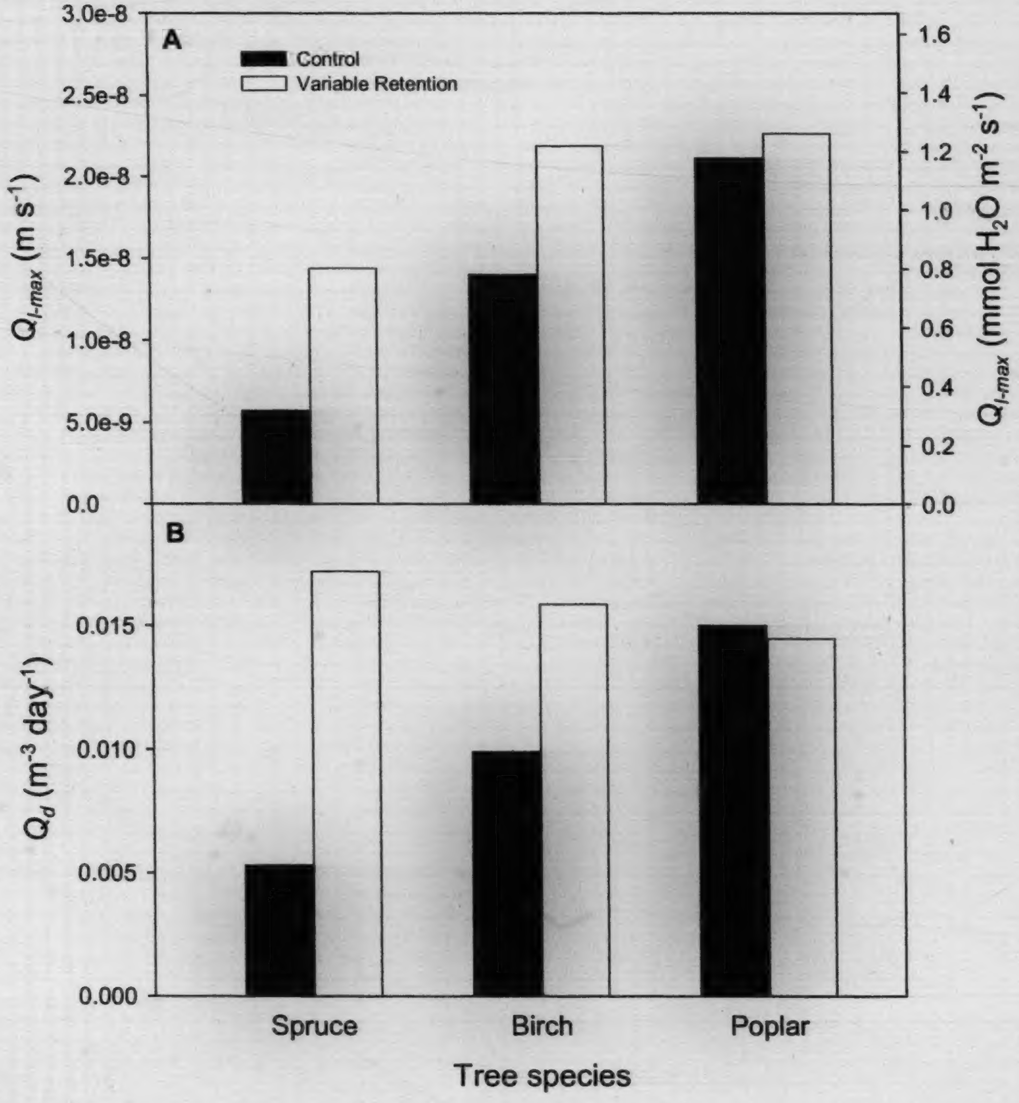


Figure 3-6. Response curves of transpiration rates per unit leaf area (Q_l) to vapour pressure deficit (D), net radiation (Q^*), wind speed (u) and potential evapotranspiration (ET_P) for white spruce, paper birch and balsam poplar from the control and variable retention sites (0900 – 1500 MDT; July 9 – August 21, 2003).

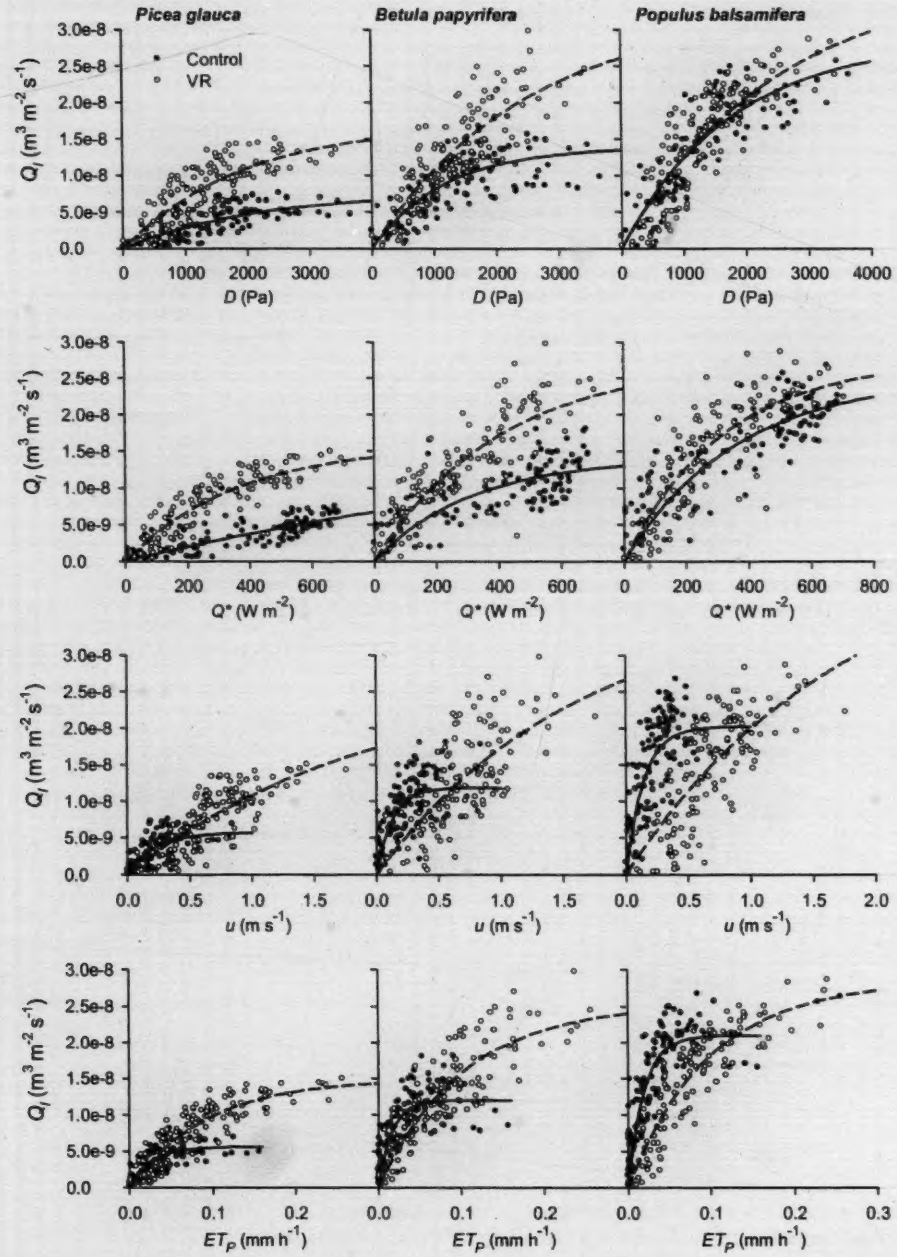


Figure 3-7. Main stem A) hydraulic conductivity (*K*$_\Psi$), B) hydraulic capacity (*Q*$_h$), and C) leaf specific hydraulic capacity (*Q*$_L$) of white spruce, paper birch, and balsam poplar trees from the control and variable retention sites (n=3).

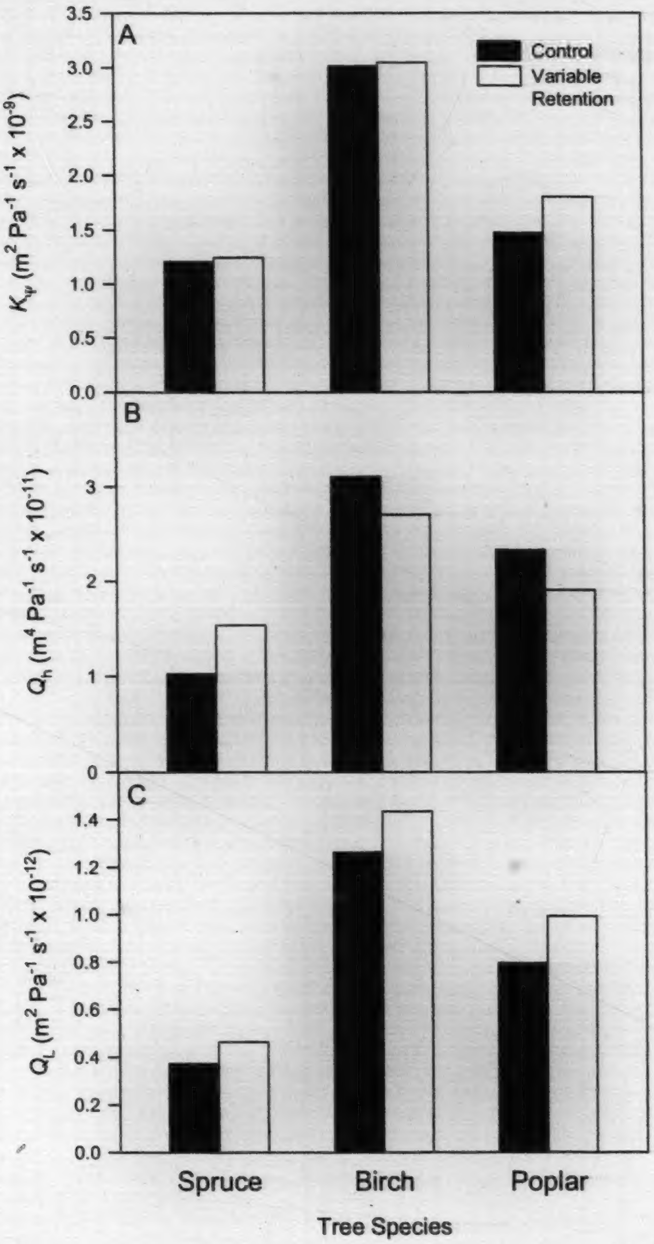
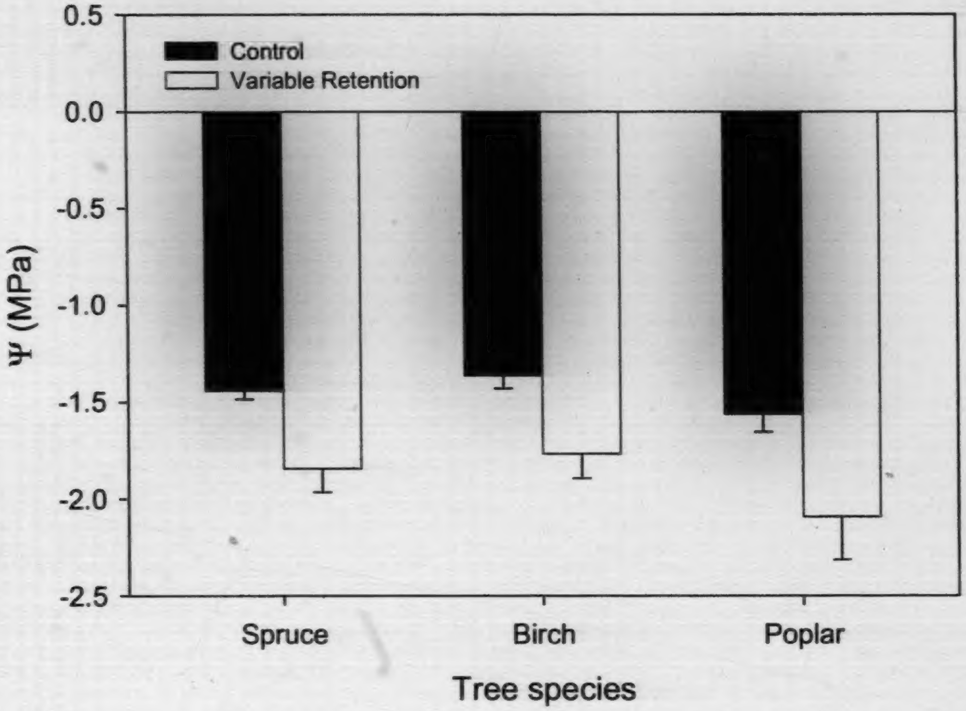


Figure 3-8. Mean total water potentials (Ψ) of white spruce, paper birch, and balsam poplar from the control and variable retention sites (July 8, 2005; n=6).



Chapter 4

CARBON ISOTOPE DISCRIMINATION AND WATER STRESS IN TREMBLING ASPEN FOLLOWING VARIABLE RETENTION HARVESTING [3]

4.1 INTRODUCTION

Although variable retention (VR) is a common harvest prescription, neither the underlying ecological assumptions nor the outcomes of this silvicultural practice have been tested thoroughly. Recent observations of VR cutovers indicate that there may be a considerable increase in stress and mortality rates of residual trees shortly after harvest, which could potentially compromise the desired biological legacy objectives of land managers (Bladon et al. In review). However, there are circumstances where the trees seem to remain healthy and persist, likely because of reduced competition for resources. The physiological response of residual trees to the abrupt change in microclimate following harvesting is likely a critical determinant in their survival and success.

Trembling aspen (*Populus tremuloides* Michx.), a species regularly retained in VR cutovers, is both ecologically and commercially the most important deciduous tree species in the North American boreal forest (Hogg et al. 2002). However, aspen mortality in VR plots was recently observed to be nearly 4-fold greater (6.1% year^{-1}) than the natural mortality rate (Bladon et al. In review). The reduced growth, dieback, and mortality of residual aspen may be attributed to the greater evaporative demand that can occur after partial harvesting, which has the potential to increase water stress and air-embolism formation in xylem vessels (Hacke and Sauter 1995, Hogg and Schwarz 1999, Frey et al. 2004, Hogg et al. 2005, Bladon et al. In press). Most often, tree response to greater evaporative demand is partial closure of stomata to maintain shoot water potential above a threshold, beyond which xylem dysfunction will occur (Tyree and Sperry 1988; Dang et al. 1997; Hogg and Hurdle 1997; Hogg et al. 2000). However, the narrowing of stomatal openings also causes a decrease in carbon fixation, limiting tree growth, and increasing the probability of whole-tree mortality (Sperry 2000, Kobe and Coates 1997).

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In C3 plants, photosynthetic activity is linked to discrimination against CO_2 containing ^{13}C by the carboxylating enzyme, Rubisco (Farquhar et al. 1982). When plant stomata are open, allowing rapid uptake of atmospheric CO_2 by leaves, ^{12}C is preferentially fixed (O'Leary 1981). Alternatively, when stomata close and resistance to CO_2 diffusion increases, proportionally more ^{13}C is incorporated into photosynthate, increasing the $\delta^{13}C$ ($^{13}C/^{12}C$ fraction) of plant material (Farquhar et al. 1989, McNulty and Swank 1995). Recent studies have taken advantage of ^{13}C fractionation to make inferences about tree stress relative to microclimatic variability. Differences in $\delta^{13}C$ have previously been explained by changes in soil moisture (Korol et al. 1999; Fessenden and Ehleringer 2003), humidity (Madhaven et al. 1991), temperature (Leavitt and Long 1986; Panek and Waring 1995), vapour pressure deficit (Francey and Farquhar 1982; Panek and Waring 1997; Bowling et al. 2002) and precipitation (MacFarlane and Adams 1998). However, I am unaware of any previous attempts to analyse the effect of VR harvesting, and the associated microclimate change, on the $\delta^{13}C$ of residual trees.

If residual aspen trees suffer from crown water stress following VR harvesting, a $\delta^{13}C$ signature should be detectable in stem growth rings. Less discrimination against ^{13}C in residual trees would provide new evidence into the mechanisms related to the crown dieback and mortality of these trees (Bladon et al. In review). The objective of this study was to quantify the $\delta^{13}C$ of stem wood in trembling aspen trees in isolated residual (IR), edge (E), and interior/control (C) positions. I hypothesized that discrimination against ^{13}C would be ranked as: C > E > IR trees. Edge trees should be subjected to less stress than IR trees because of the greater shelter from wind. Secondly, as cut trees were skidded to the centre of the block, the E trees likely experienced reduce damage to roots from skidding traffic that the IR trees. To explore if VR would subject residual trees to greater stress in more xeric regions, I analysed the differences in $\delta^{13}C$ across a continental precipitation gradient. I hypothesized that trees in the drier regions would have greater $\delta^{13}C$, and more water stress, than trees from regions with higher precipitation. Finally, I hypothesized slender trees would have greater $\delta^{13}C$ than stout trees following VR, because of the greater potential for xylem damage in slender trees due to increased wind exposure and bending (Fredericksen 1994, Liu et al. 2003).

4.2 MATERIALS AND METHODS

4.2.1 Study Site Descriptions

Research occurred near Calling Lake (55° 15′N, 113° 10′W) and Drayton Valley (53° 13′N, 114° 59′W), Alberta, and at the Lac Duparquet Research and Teaching Forest (FERLD) in north-western Quebec (48° 46′N, 79° 26′W), which represent three distinct climatic regions (Table 4-1). All research plots were in boreal mixedwood forest, with various mixtures of trembling aspen, white birch (*Betula papyrifera* Marsh.), balsam poplar (*Populus balsamifera* L.), balsam fir (*Abies balsamea* L.), black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss) and jack pine (*Pinus banksiana* Lamb.).

4.2.2 Field Sampling

In Spring 2004, mature aspen trees were sampled from 7 cutover areas (4 years-old) and adjacent, unharvested forests in each region. Xylem samples were collected in each plot from 8 isolated residual trees, 8 edge trees and 8 interior (control) trees, for a total of 504 trees (168 per region). At each location, 4 trees with high slenderness coefficient (SC = height/dbh; SC ≥ 90) and 4 trees with low slenderness coefficient (SC < 90) were sampled. Isolated residuals included single trees, or those in small patches of trees (< 10 trees), left standing in the harvested area (minimum 4 tree lengths from the cutblock edge). Edge trees were selected randomly from the south-facing edge of the cutover. Control trees were selected at a distance of approximately 50 m of contiguous forest adjacent to the cutover to minimize edge influence. All trees were older than 30 years to avoid the "juvenile effect", an increasing $\delta^{13}C$ trend with time (Francey and Farquhar 1982). I selected trees of similar size, shape, and growth conditions to ensure an accurate relationship between $\delta^{13}C$ and microclimate (Panek and Waring 1995). Trees displaying signs of pathogens, insect defoliation, or bole damage from harvesting equipment were not selected. Measurements were recorded for height, diameter at breast height (dbh), crown class (CC), height to live crown (htlc), crown radius, and SC for each tree. Assuming the tree crowns were parabloids, crown volume (V; m^3) was estimated as:

Equation 4-1 $$V = \frac{\pi d_b^2 L}{12}$$

where d_b is the diameter (m) of the crown at its base and L is the crown length (m).

4.2.3 Carbon Isotope Analysis

Xylem samples (~5 x 5 cm) were collected at 1.3 m height, using a hammer and a chisel. To ensure samples included pre- and post-harvest annual rings at least 15 annual rings were collected. In the laboratory, 3 years of pre-harvest annual rings (1997-1999) and 3 years of post-harvest annual rings (2001-2004) were carefully excised from each sample. Wood from the year of harvest (2000) was not included due to the potential for some carry-over signal from the previous year, which could confound the results. Samples from 4 trees in the same position (isolated residual, edge or interior), slenderness class (slender or stout) and same time-period (before and after VR) were pooled together (Leavitt and Long 1984). Pooled samples were oven-dried at 65°C for 72 h and ground with a Wiley mill (40 mesh) prior to holocellulose extraction for stable carbon isotope analysis by a modified version of the "Jayme-Wise" method (Leavitt and Danzer 1993). Isolated holocellulose was ground with a ball grinder and analysed with a mass spectrometer for the $^{13}C/^{12}C$ ratio. The carbon isotope ratios ($\delta^{13}C$) with respect to the same ratio of the Pee Dee Belemnite (PDB) carbonate standard were calculated as:

Equation 4-2
$$\delta^{13}C = \left(\frac{{}^{13}C/{}^{12}C_{sample}}{{}^{13}C/{}^{12}C_{PDB}} - 1 \right) \times 1000‰$$

where $\delta^{13}C$ is expressed in permil (‰) units. During holocellulose extraction, samples were also soaked in bleach solution (1 hr.), centrifuged and weighed to determine the lignin content.

4.2.4 Foliar Nitrogen Analysis

I measured foliar nitrogen concentration [N] from 2 slender and 2 stout isolated residual trees, in each of the 7 stands in the Drayton Valley study area, as an indicator of photosynthetic capacity (Livingston et al. 1998). Foliage was collected with a shotgun in summer 2005 from relatively exposed, south-facing branches located in the middle or upper third of the crown. Samples were dried at 65°C for 72 h, ground with a Wiley mill (40 mesh) and evaluated with an auto-analyser.

4.2.5 Statistical Analysis

Differences in $\delta^{13}C$ values between the three regions and between the interior, edge and isolated residual trees both before and after VR harvesting were tested as a randomized block, split-split-split plot design. Region (Calling Lake, Drayton Valley and Lac Duparquet), slenderness class (slender and stout) and tree position (interior, edge and residual) were the fixed main plot effects, while time (before and after VR) was the fixed subplot effect. Analysis of variance (ANOVA), with a Tukey multiple comparisons test, was used to analyze this design (SAS Version 9.1, SAS Institute Inc., Carey, NC). A paired two-tailed t-test was used to compare foliar [N] between slender and stout trees.

4.3 RESULTS

I observed a difference in overall mean $\delta^{13}C$ between control (C), edge (E) and isolated residual (IR) trees in all 3 regions combined after VR harvesting ($P < 0.0001$), but not before the treatment ($P = 0.48$). The overall $\delta^{13}C$ in the three years before the harvest was -25.76‰ ± 0.11 in the C trees, -25.63‰ ± 0.11 in the E trees, and -25.68‰ ± 0.11 in the IR trees. In the 3 years after VR harvesting, the general pattern of $\delta^{13}C$ was IR (-24.78‰ ± 0.11) > E (-25.31‰ ± 0.12) > C (-25.71‰ ± 0.12).

In each region separately, variation in carbon isotope discrimination due to tree position was also evident (Calling Lake $P = 0.03$; Drayton Valley $P < 0.01$; Lac Duparquet $P < 0.001$) (Figure 4-1). This difference was not present prior to VR in any region (Calling Lake $P = 0.58$; Drayton Valley $P = 0.96$; Lac Duparquet $P = 0.65$). The interaction of time and position was also significant in all 3 regions ($P < 0.001$), indicating that a change in carbon isotope discrimination occurred between the control, edge and isolated residual positions after VR harvesting.

The general regional pattern of $\delta^{13}C$ was: Calling Lake > Drayton Valley > Lac Duparquet (Figure 4-1), which was the inverse of the regional precipitation gradient (Calling Lake < Drayton Valley < Lac Duparquet) (Table 4-1). The increase in $\delta^{13}C$ with decreasing precipitation was consistent in all three tree positions before and after VR harvest (Figure 4-2). Carbon isotope ratios before VR harvest were -25.13‰ ± 0.08 in Calling Lake, -25.94‰ ± 0.10 in Drayton Valley and -26.05‰ ± 0.08 in Lac Duparquet. After VR harvest the mean $\delta^{13}C$ increased in all 3 regions (Calling Lake = -24.76‰ ± 0.10; Drayton Valley = -25.35‰ ± 0.14; Lac Duparquet = -25.78‰ ± 0.11). Regionally, these differences in carbon isotope discrimination were significant both before ($P <$ 0.0001) and after harvest ($P < 0.0001$).

Despite small differences in tree age among regions, differences in precipitation and regional $\delta^{13}C$ discrimination were strongly correlated with differences in tree size among regions (Table 4-2). Regionally, the trend in tree height and dbh was Lac Duparquet > Drayton Valley > Calling Lake. Additionally, trees in Lac Duparquet supported more crown volume than trees in Drayton Valley (2.3-times more) and Calling Lake (2.8-times more). I found no differences in slenderness coefficient between the regions. There was minimal difference in tree heights between slender and stout trees in each region; however, the mean dbh was typically much smaller for slender trees in all three regions. Stout trees generally supported 2.1- to 2.7-fold more crown volume than slender trees.

I observed a general pattern of less discrimination against ^{13}C by stout trees (SC < 90) than slender trees (SC ≥ 90), both before and after VR harvesting. Overall, $\delta^{13}C$ of slender trees increased from -25.78‰ ± 0.08 (pre-harvest) to -25.43‰ ± 0.10 (post-harvest). Stout trees had a slightly greater increase in $\delta^{13}C$, from -25.54‰ ± 0.10 (pre-harvest) to -25.10‰ ± 0.11 (post-harvest). The mean increase in $\delta^{13}C$ in Drayton Valley was 1.28‰ for stout trees and 1.13‰ for slender trees (Figure 4-3). In Calling Lake, the increase in $\delta^{13}C$ was most noticeable in the stout IR trees, with a mean increase of 0.89‰, while slender trees increased only 0.36‰ after the VR harvest (Figure 4-3). Alternatively, in the Lac Duparquet IR trees I observed a mean increase in $\delta^{13}C$ of 0.86‰ in slender trees and 0.63‰ in stout trees (Figure 4-3). In both Calling Lake and Drayton Valley, the difference in $\delta^{13}C$ between slender and stout trees was not significant pre-harvest (CL: $P = 0.76$; and DV: $P = 0.15$), but was significant in the 3 years after the VR harvest (CL and DV: $P = 0.05$). There was no difference in carbon discrimination between slender and stout isolated residual trees in Lac Duparquet, either before ($P = 0.72$) or after the VR harvest (QC: $P = 0.35$).

I found no trend in the cellulose to lignin ratio between pre- and post-harvest samples ($P = 0.33$) or between the different trees positions ($P = 0.97$). The nutritional analysis showed that the foliar nitrogen concentration [N] was 1.71% ± 0.17 for slender trees and 1.77% ± 0.15 for stout trees, and these were not significantly different ($P = 0.47$).

4.4 DISCUSSION

In the three years after variable retention (VR) harvesting, the abundance of ^{13}C (expressed as δ^{13}C) in the wood of trembling aspen residual trees was consistently greater than in the wood of trees in the other positions (i.e. edge and control) (Figure 4-1). In all three regions, trees on the edge of the cutblocks had intermediate discrimination against ^{13}C, between the isolated residual and control trees. This provides evidence that the residual and edge trees suffered from water stress after the disturbance, since there was no difference in δ^{13}C between the trees in the different positions prior to VR harvesting. I suggest that increased potential evapotranspiration at the crown level following VR is responsible for stomatal closure and enhanced δ^{13}C in the residual and edge trees. This is a plausible explanation, because aspen, like other hardwoods are known to be highly susceptible to xylem dysfunction (Sperry et al. 1991, Sperry and Sullivan 1992). Therefore, they possess stomata which are sensitive to changes in evaporative demand in order to maintain leaf and stem water potential above a critical threshold to avoid xylem cavitation (Dang et al. 1997). Aspen have previously been observed to reduce stomatal conductance following an increase in atmospheric drought stress (Hogg and Hurdle 1997, Hogg et al. 2000). Additionally, when the majority of the forest canopy in a given area is removed, potential evapotranspiration at the crown level generally rises (Zheng et al. 2000, Bladon et al. In press). However, plant responses to the change in microclimate after VR are likely to be related to their stomatal sensitivity, resistance to xylem dysfunction, as well as the local site conditions (Picon et al. 1996, Zhang et al. 1997, Martinenz-Vilalta et al. 2004). For instance, similar to this study, there have been observations of increased $\delta^{13}C$ in plant tissue from *Pinus pinaster* and *Pinus radiata* with decreased stand density (Walcroft et al. 1996, Warren et al. 2001). However, others have shown increased rates of photosynthesis and greater discrimination against ^{13}C by a coniferous species, ponderosa pine (*Pinus ponderosa*) in response to a thinning experiment (61 – 82% basal area removed) (McDowell et al. 2003).

The greater discrimination against ^{13}C by edge trees than residual trees indicates that there is potentially some sheltering effect of the adjacent contiguous forest, which can limit water stress in these trees. My findings of lower $\delta^{13}C$ in edge trees than residuals provides important insight, which may be relevant to the different responses between trees aggregated in residual patches, and trees dispersed throughout a cutblock. If high dieback and mortality threaten the objectives of providing a living legacy through VR, then perhaps leaving larger patches may provide improved and adequate shelter to reduce atmospheric moisture stress, crown dieback and possibly mortality of residual trees. The sheltering effect of edges, and potentially patches, is likely to produce lower evaporative demand than in exposed cutblocks, due to lower air temperatures, wind speeds, radiation and/or higher relative humidity (Chen et al. 1995). This suggestion is supported by research from an Amazonian lowland rainforest, which reported no difference in canopy foliar $\delta^{13}C$ between edge trees and trees in 1-ha forest fragments (Kapos et al. 1993).

Another possible explanation for the difference in $\delta^{13}C$ between E and IR trees is related to soil compaction and root damage. It is likely that IR trees were subjected to greater heavy equipment traffic during the harvesting operations than edge trees, resulting in altered soil properties and reduced plant-available water (Greacen and Sands 1980, Kozlowski 1999, Gomez et al. 2002). Thus, soil compaction could also influence $\delta^{13}C$ by creating greater water stress for IR trees than E trees. These results could also provide an indication of how residual trees aggregated in patches may respond to VR harvesting. Similar to E trees, I would expect trees in patches to be subjected to less heavy equipment traffic than IR trees and thus, less risk of soil compaction and water stress.

My study also found a regional trend in carbon isotope ratios, with the $\delta^{13}C$ in Calling Lake > Drayton Valley > Lac Duparquet, both before and after VR (Figure 4-1). This regional trend in $\delta^{13}C$ was strongly related to the mean annual precipitation gradient (Calling Lake < Drayton Valley < Lac Duparquet) (Figure 4-2). These results indicate that water stress following VR in residual and edge trees is likely to be a greater concern in more xeric regions, where trees may already be showing signs of atmospheric moisture stress prior to harvest, compared to moister regions. Additionally, even though trees in Lac Duparquet had to supply water to crown volumes 2.1- to 2.7-fold greater than in the other regions, these trees showed less stress than trees in the drier regions. This was possibly due to a lower evaporative demand in this region, owing to the much higher precipitation (Table 4-1), and likely higher relative humidity.

Elevated $\delta^{13}C$ in aspen in the drier regions was expected. This was consistent with previous reports of a ^{13}C trend in various woody species which was related to annual precipitation gradients, and attributed to increasing stomatal closure in the more arid regions (Stewart et al. 1995, Schulze et al. 1998, Miller et al. 2001, Bowling et al. 2002). Within regions, it has also been observed that years with the greatest atmospheric or soil moisture stress correspond with the highest $\delta^{13}C$ values in ring cellulose (Leavitt 1992).

Regional differences in climate were also strongly related to differences in mean tree crown volume and tree size among the three regions. Increased mean annual precipitation along the climatic gradient from Calling Lake to Lac Duparquet was strongly associated with reduction in regional mean tree water stress ($\delta^{13}C$) and increased site productivity, as reflected in mean tree height, diameter, and crown volume. This provides additional support for the notion that regional hydro-climate plays a strong role governing regional growing season stress and forest productivity (Grier and Running 1977).

Contrary to my expectation, I found a general trend of greater $\delta^{13}C$, and indication of more water stress, in stout trees than slender trees in all regions, both before and after VR (Figure 4-3). This was in contrast to the idea that trees with more bending stress would suffer greater damage to xylem permeability than more rigid trees, due to greater wind following VR (Frederickson et al. 1994). I believe that the stout trees probably suffered greater water stress because they supported 2- to 3-times more crown volume compared to the slender trees (Table 4-2). Thus, stout trees likely had much higher water demand per unit leaf area than the slender trees. Additionally, less dominant trees have been observed to have greater stem hydraulic capacity per unit leaf area, improving their ability to survive short-term water stress compared to dominants (Reid et al. 2003). Following VR, stout trees located on the edge of cutovers, and as isolated residuals, had larger increases in $\delta^{13}C$ than slender trees in the same locations (Figure 4-4). This suggests that stout aspen trees, with large crowns, left as residuals are likely to suffer greater water stress than slender trees following VR. I believe this could be due to their inability to transport sufficient water to the large volume of foliage. However, in a related study I found no relationship between residual tree mortality and slenderness (Bladon et al. In review). Thus, while stout trees could suffer greater short-term water stress following VR, a combination of other factors (e.g. hydraulic characteristics, root structure, soil moisture, nutrient regime) likely determine the post-harvest fate of an individual residual tree.

In summary, my results suggest that trees are under increasing water stress after VR harvesting (IR > E > C). The results from edge trees indicate that leaving broadleaf residuals in larger patches or more sheltered landscape positions could potentially reduce the atmospheric moisture stress on these trees, ultimately reducing dieback and mortality. My study also showed that this is likely to be a more critical problem in drier regions, where trees may already be water stressed prior to the harvest. Finally, my study also found that stout trees may suffer greater short-term water stress than slender trees. I believe this may occur because stout trees often must maintain a water supply to a considerably larger volume of leaf area than slender trees.

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Table 4-1. Environmental characteristics of the three boreal mixedwood regions sampled for $\delta^{13}C$ analysis.

Characteristic	Calling Lake, Alberta	Drayton Valley, Alberta	Lac Duparquet, Quebec
Site location (latitude and longitude)	55° 30'N, 113° 40'W	53° 13'N, 114° 59'W	48° 30'N, 79° 22'W
Elevation (m)	550 - 650	900 - 1000	250-300
Dominant soils	Luvisolic	Luvisolic	Luvisolic
Parent material	Glaciolacustrine	Morainal till	Glaciolacustrine
Long-term mean daily temperature (°C)	0.9	2.3	0.7
Pre-harvest (1997-1999; °C)	2.3	1.5	3.3
Post-harvest (2001-2003; °C)	1.0	1.5	2.7
Mean maximum daily temperature (°C)	7.2	9.1	6.9
Mean minimum daily temperature (°C)	-5.3	-4.6	-5.4
Long-term annual precipitation (mm)	454	535	890
Pre-harvest (1997-1999; mm)	370.8	564.4	809.5
Post-harvest (2001-2003; mm)	393.5	504.1	808.1

Table 4-2. Mean characteristics and standard errors of trembling aspen sample trees from the three boreal mixedwood regions used for $\delta^{13}C$ analysis.

Characteristic		Calling Lake, AB	Drayton Valley, AB	Lac Duparquet, QC
Age (years)		58.0 ± 2.0	72.2 ± 3.7	67.5 ± 1.00
Height (m)		20.6 ± 0.22	22.4 ± 0.29	26.2 ± 0.29
	Slender	20.8 ± 0.33	22.1 ± 0.45	25.5 ± 0.47
	Stout	20.5 ± 0.28	22.7 ± 0.35	26.4 ± 0.35
dbh (cm)		24.9 ± 0.45	27.3 ± 0.64	31.8 ± 0.71
	Slender	21.1 ± 0.32	22.0 ± 0.50	24.7 ± 0.66
	Stout	28.7 ± 0.59	32.5 ± 0.86	37.0 ± 0.70
Crown length (m)		8.15 ± 0.18	8.73 ± 0.19	10.85 ± 0.36
	Slender	7.82 ± 0.27	7.6 ± 0.25	8.6 ± 0.66
	Stout	8.49 ± 0.24	9.4 ± 0.27	11.7 ± 0.41
Crown radius (m)		2.13 ± 0.044	2.18 ± 0.059	3.11 ± 0.083
	Slender	1.77 ± 0.043	1.80 ± 0.059	2.29 ± 0.15
	Stout	2.45 ± 0.13	2.55 ± 0.095	3.40 ± 0.090
Crown volume (m^3)		45.42 ± 3.06	55.18 ± 5.00	128.62 ± 8.82
	Slender	28.88 ± 2.38	31.35 ± 2.93	57.80 ± 8.04
	Stout	61.91 ± 5.03	79.02 ± 8.85	154.01 ± 10.60
Slenderness coefficient		85.8 ± 1.24	86.6 ± 1.40	84.3 ± 1.54

Figure 4-1. A comparison of the mean stable carbon isotopic composition ($\delta^{13}C$) between control, edge and isolated residual trees in Calling Lake (CL), Drayton Valley (DV) and Lac Duparquet, Quebec (QC) both A. pre- and B. post-VR harvest.

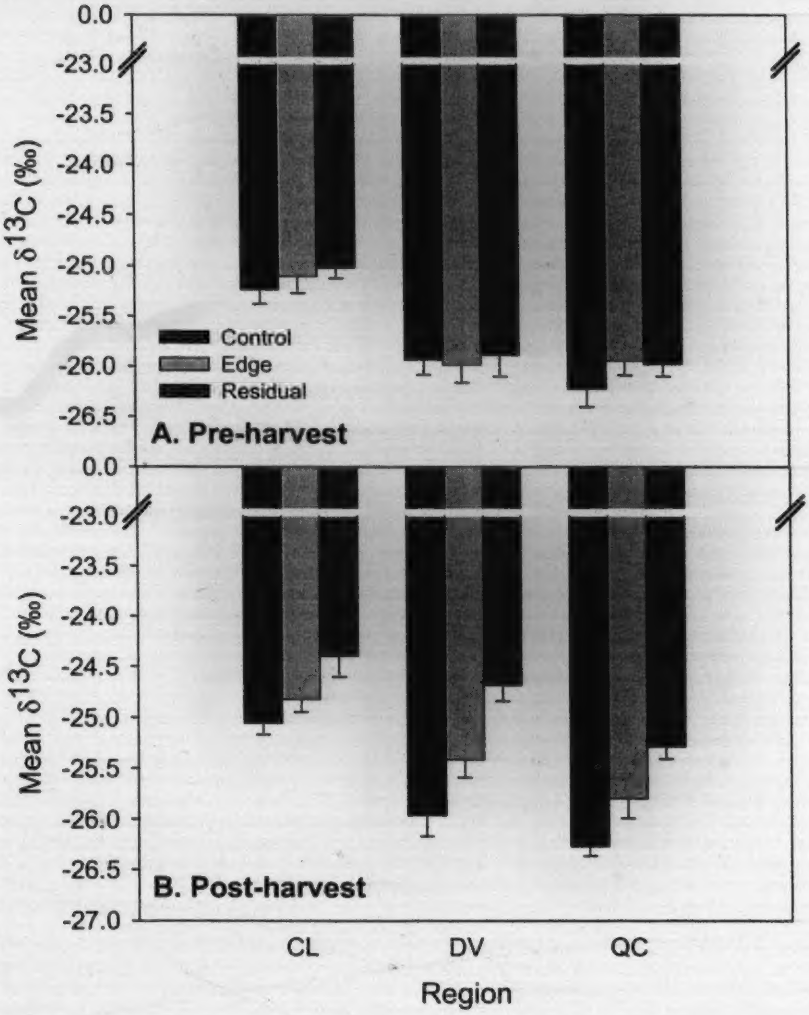


Figure 4-2. A comparison of the mean annual precipitation (mm) from Calling Lake and Drayton Valley, Alberta and Lac Duparquet, Quebec to the mean stable carbon isotopic composition ($\delta^{13}C$) from A. control (pre- $R^2 = 0.80$; post $R^2 = 0.89$), B. edge (pre- $R^2 = 0.78$; post $R^2 = 0.80$), and C. isolated residual (pre- $R^2 = 0.78$; post $R^2 = 0.92$) trembling aspen before and after VR harvesting.

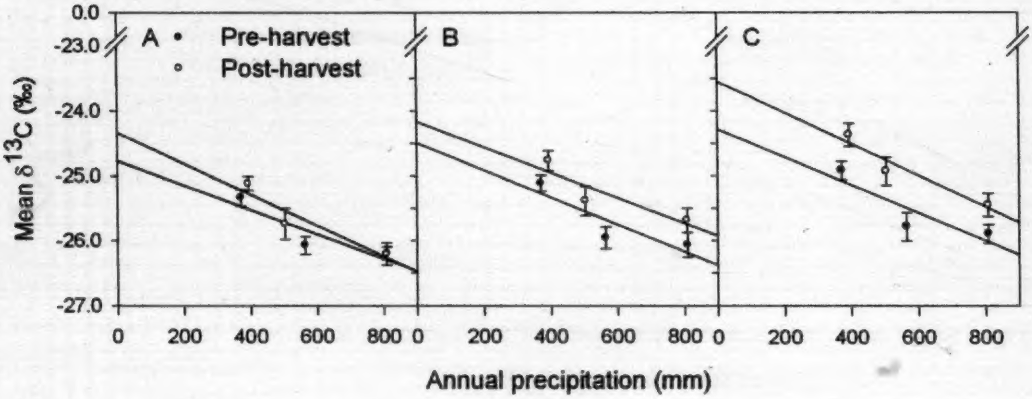


Figure 4-3. Mean stable carbon isotopic composition ($\delta^{13}C$) for slender and stout isolated residual, trembling aspen trees. A. Pre- and B. post-VR harvest in Calling Lake (CL) and Drayton Valley (DV), Alberta and Lac Duparquet, Quebec (QC).

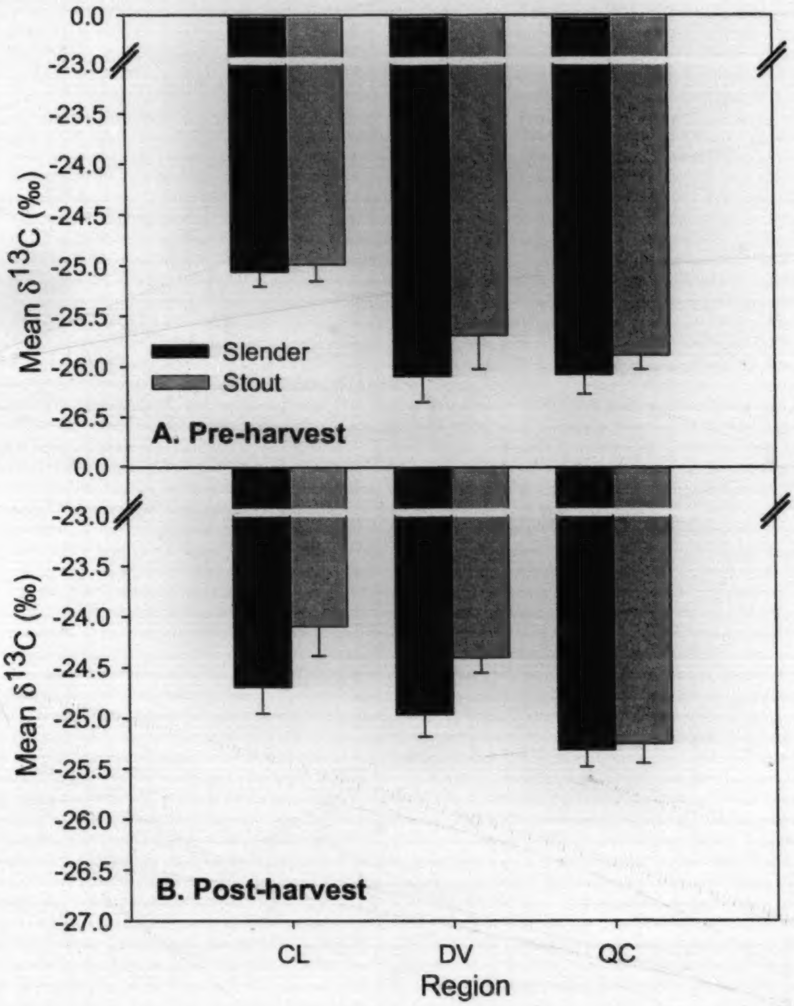
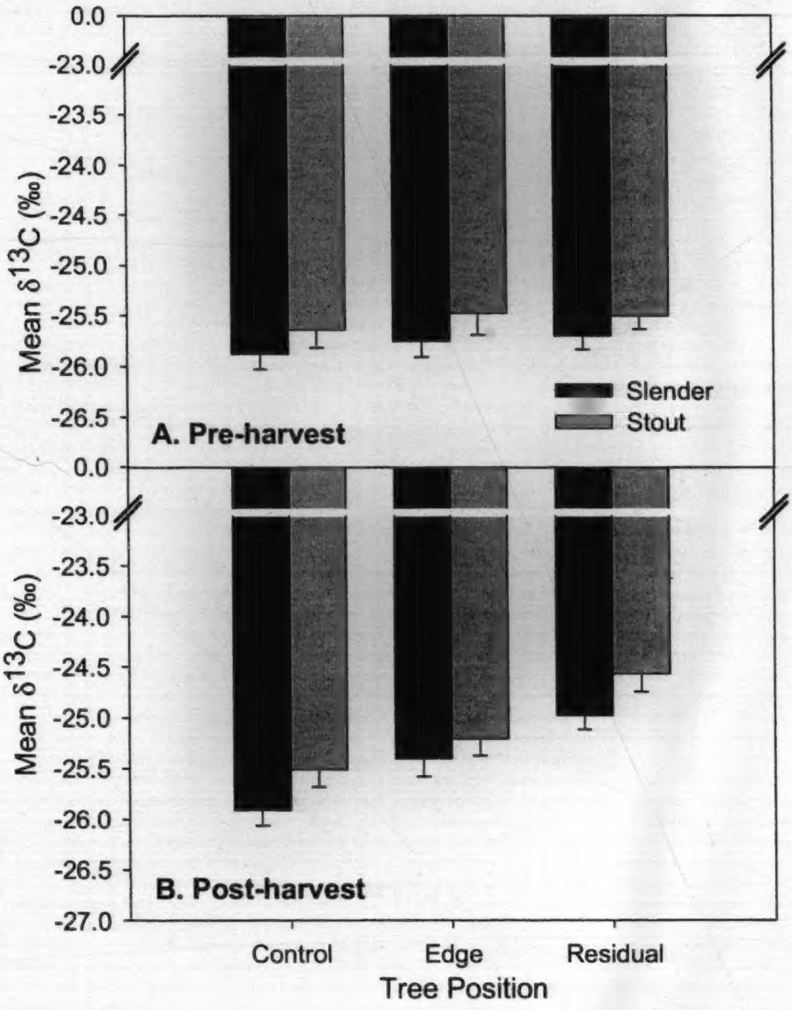


Figure 4-4. Mean stable carbon isotopic composition ($\delta^{13}C$), of slender and stout trees from control, edge and isolated residual trembling aspen trees, A. pre- and B. post-VR harvest in Calling Lake and Drayton Valley, Alberta and Lac Duparquet, Quebec.



Chapter 5

SYNTHESIS

Forest managers are increasingly challenged to integrate multiple, and often conflicting, forest management objectives into new silvicultural systems. The present philosophy of ecosystem management demands a balance between protecting natural systems and using them to meet growing societal demands. Variable retention (VR) harvesting is a silvicultural tool designed to minimize harvesting impacts on forest ecological integrity, through the retention of structural elements for the maintenance of biological diversity and ecosystem function. While this practice has been broadly implemented as the primary silvicultural system in many parts of the world, there is still a wide array of uncertainties regarding its effectiveness.

The purpose of this research was to address the uncertainties regarding the premature mortality of residual trees shortly after VR harvesting of boreal mixedwood forests. To my knowledge, this dissertation represents the first study to quantify the mortality rates of residual trees, and then attempt to explain why the trees may be dying prematurely. Additionally, this study is the first to attempt to explore various physiological responses (i.e. transpiration rates, carbon isotope discrimination) of several boreal tree species to VR harvesting. I believe the results of this dissertation provide important knowledge that will help address the three central questions for developing guidelines for VR harvesting practices (Franklin et al. 1997): what to retain, how much to retain, and what is the most appropriate spatial pattern for retention to meet the desired objectives?

5.1 PREMATURE RESIDUAL TREE MORTALITY

My results indicated that dispersed residual trees could be highly susceptible to premature mortality shortly after VR harvesting (Figure 2-1). High mortality of residual trees should be a concern for managers who are using VR as an approach to land management that is considered as a disturbance that has similar effects to those of natural disturbances (i.e. wildfire). Following natural disturbances, relatively small amounts of organic matter actually are consumed or removed from the site (Franklin et al. 1997). Further, after most of these events there is a broad range of live mature trees, standing dead trees (snags), and tree boles and other woody debris on the ground that provide essential habitat for biodiversity and sustain other critical ecosystem functions.

Currently, the majority of forest companies retain fewer live trees in a more dispersed pattern than remain post-fire (Smyth et al. 2005). If VR is to be truly sustainable, and guided by the natural disturbance dynamics of wildfire, then at the landscape level, post-VR sites should contain a similar range of stand areas covered by live trees as observed post-fire. Studies of post-fire sites across several regions have shown a diverse range in the percentages of fire area covered by living residual trees: $\bar{X}$ = 26% (range: 0–98%; Smyth et al. 2005), $\bar{X}$ = 22% (range: 0–50%; Andison 2001), $\bar{X}$ = 6% (range: 1–16%; Smyth 1999), $\bar{X}$ = 13% (range: 1–25%; Stuart-Smith and Hendry 1998), $\bar{X}$ = 2% (Eberhart and Woodard 1987), and range = 3–15% (DeLong and Tanner 1996). Additionally, studies in the boreal forest of Alberta have shown that fire intensity is typically lower in mixedwood stands than in other forest types (Cumming 2001). Therefore, more stand area is typically covered by live residual trees post-fire in these forest types, which should be reflected in VR if the practice is to be sustainable. Thus, even if post-fire mortality rates of residual trees are similar to the high post-VR mortality rates I observed in my study, the current level of retention in VR may be insufficient to maintain ecosystem function. However, social and economic constraints may influence the decisions of land managers, which is contrary to the philosophy of sustainability which seeks a complete balance and integration of the social, economic, and ecological values in all management decisions.

At the stand level, the implications of high mortality of residuals will depend on the defined forest management objectives. For instance, if VR is implemented to provide mature forest habitat, greater variability in tree sizes and ages, provide more complex horizontal and vertical canopy structure, or to enhance long-term forest recovery by providing a seed source, then mortality rates similar to those found in this research raise concern that these objectives may not be attainable. Thus, future guidelines for acceptable levels of retention should reflect the likelihood of high mortality in many VR cutovers in the first years after harvest. It may be critical for particular biodiversity objectives, either to retain a greater number of residual trees in the cutover or to retain trees most likely to survive.

However, from a broad ecological view, long-term survival of retention trees may not always be critical. Living trees, standing dead trees (snags) and downed logs all provide important pieces of the structural legacy that separates mature forests from early successional forests (Beese et al. 2003, Deans et al. 2003). Thus, in some cutovers a certain amount of snag creation and windthrow will be desirable, while in others a higher density of standing live trees may be necessary. No single prescription, configuration or amount of retention will meet all objectives equally well (Aubrey et al. 2004). Ultimately, the optimal levels of retention are likely to depend on regional and local site conditions (i.e. slope, aspect, elevation) (Zenner 2000). In fact, in order to generate more variation in disturbance severity, quality, area, and repeatability to restore some of the fundamental characteristics of the natural forests' multiscale heterogeneity, a diverse array of silvicultural and harvesting treatments, as guided by natural disturbance dynamics, is desirable (Kuuluvainen 2002). In general, the more heterogeneous the structure retained from the original forest, the more closely the VR approach is to approximate a natural disturbance (Mitchell and Beese 2002).

5.2 SPECIES DIFFERENCES IN MORTALITY MECHANISMS

My work showed strong differences between the hardwoods and the conifer residual trees in the way that the trees died. For instance, the majority of aspen, birch, and poplar residuals were found dead as standing snags, while the majority of spruce died due to windthrow. It is likely that the broadleaf trees were more susceptible to dieback and standing mortality due to a different ecophysiological response to the abrupt change in microclimate after VR harvesting than the conifers. This important finding may aid land managers in selecting the appropriate mix of trees to retain to meet specific objectives. For instance, if snag recruitment is a primary objective, then leaving many isolated hardwoods would be a good strategy. Conversely, if a rapid input of coarse woody debris is desirable then more spruce could be retained during VR harvest. I have used my results to make some predictions about the most likely dominant outcomes for several of the important boreal mixedwood tree species if retained as dispersed residuals following VR harvesting (Table 5-1). While these predictions are somewhat speculative, they may assist land managers in the most appropriate approach to VR harvesting (e.g. dispersed vs. aggregate, species composition) to achieve certain objectives.

A more detailed examination of the mechanisms potentially leading to mortality can provide information into the different spatial patterns the various species could be retained in to meet additional objectives. For example, there are several lines of evidence from my work showing that much of the dieback and mortality of the broadleaf residuals may be due to atmospheric moisture stress. This evidence includes, constrained Q_l (Figure 3-4) despite large increases in ET_P (Figure 3-3), more negative Ψ (Figure 3-8), and increased $\delta^{13}C$ (Figure 4-1) in residual broadleaf trees when compared with control trees. However, the $\delta^{13}C$ indicated that trees on the edges of cutovers were less stressed than isolated residuals, perhaps due to some sheltering effect of the adjacent, contiguous forest. Thus, if the management objective is to limit stress on the broadleaf trees in hopes of their survival, then retaining them in larger patches or more sheltered landscape positions may provide adequate shelter from the abrupt change in microclimate.

For spruce, this research showed that the most dominant residuals were the most susceptible to windthrow. I also found that as mechanical damage to the main bole increased, the more likely a residual spruce was to fall due to windthrow. The risk of windthrow is likely more complex than these results suggest. Complex interactions between wind and stand factors such as canopy height, root systems, soil properties, root rot, crown length, pre-harvest stand density, and slope position are all likely to influence windthrow (Mitchell 1995, Ruel 1995, Ruel et al. 1997). However, our results indicate that leaving smaller, undamaged, and more windfirm spruce may be more likely to result in living trees, if this is an objective.

Tree mortality is particularly complex, influenced by a variety of factors, including the environment, random events, physiology, successional development, and tree age (Keane et al. 2001). The complexities of the mortality mechanisms provide challenges to definitively separate the ultimate and proximal causes of tree death (Franklin et al. 1987). The intricacy of Alberta's boreal mixedwood forests offer additional challenges to understanding mortality mechanisms (Yao et al. 2001). Thus, mortality of both residual trees and trees in closed-canopy stands remains a poorly understood process, rarely observed directly in the field (Wyckoff and Clark 2000). However, if forest management decisions are to be sustainable, it is imperative that we advance the knowledge of the fundamental processes governing premature tree mortality (Yang and Titus 2002). Consequently, my study provides important, fundamental information about species differences in mortality mechanisms. Nevertheless, further research is necessary to continue to improve our understanding of tree mortality.

5.3 MICROCLIMATE CHANGE AFTER VR

This was the first study to quantify and demonstrate that VR harvesting can dramatically alter the microclimate at the crown level. Specifically, I observed a nearly three-fold increase in potential evapotranspiration (ET_P) in the VR site (Figure 3-3), which appeared to be driven primarily by a considerable increase in wind speed. This finding was consistent with others, who have observed similar increases in wind speed following partial harvesting (Rudnicki et al. 2003). Additionally, I found physiologically neglible difference in air temperature, relative humidty or vapour pressure deficit at the crown level following VR harvesting (Figure 3-1). However, this was in contrast to many authors who have shown lower relative humidity and increased air temperatures and vapour pressure deficits at positions near ground level (0.2 m) after partial harvesting (Matlack 1993, Chen et al. 1995, Man and Lieffers 1999, Barg and Edmonds 1999, Chen et al. 1999, Zheng et al. 2000). These discrepancies in observations further illustrate the complex and dynamic nature of microclimatic response to forest canopy removal. My work also highlights the likelihood of vertical gradients in microclimate and in the importance of placing sensors at the appropriate canopy height to form inferences about plant responses.

5.4 DIFFERENTIAL WATER USE

External to the issue of VR harvesting, this study provides a significant contribution to the literature with insights into the differential transpiration rates and daily water use of 3 important boreal tree species. Only recently have techniques that allow quantification of water movement through sapwood xylem become broadly available and employable (Cermák et al. 1973, Cermák et al. 1976, Granier 1985, Granier 1987). These methods were used to provide new insights into the dynamics of transpiration by mature white spruce, paper birch and balsam poplar trees.

My results indicate that hardwood species may transpire a greater volume of water per unit leaf area than conifers (Figure 3-4). However, when evaporative demand increased, it appeared that the broadleaf trees had a greater ability to control Q_l by the behaviour of stomata. This was likely due to their high susceptibility to cavitation and their need to maintain Ψ above a critical threshold level (Tyree et al. 1994). Alternatively, spruce may be able to increase their water use as evaporative demand increases, with little risk of cavitation due to comparatively low sap fluxes and high cavitation resistance (Maherali et al. 2004). This knowledge could help in accurately assessing and managing local and regional water budgets. For instance, a management plan to leave a riparian buffer comprised of primarily spruce trees could have large and undesirable impacts on the water resources if the residual trees greatly increase their transpiration rates following harvesting. In this example, a potentially wider buffer, to limit the microclimate change to streamside trees, may be necessary to protect the water resource.

5.5 RESEARCH NEEDS

The variable retention approach to harvesting forests is a relatively new and untested silvicultural system. Thus, several important scientific and technical issues must be addressed to improve VR harvesting and to ensure that this practice will enable land managers to meet their desired objectives:

- This was the first study to attempt to quantify mortality rates of residual trees following VR harvesting and determine why the trees are dying. While the study has provided much new evidence that the mortality may be related to xylem dysfunction due to increased atmospheric moisture stress, it remains unclear why some broadleaf trees are able to remain healthy and persist, while others suffer extensive dieback and mortality. One possible explanation is the root damage and soil compaction associated with normal harvesting operations, resulting in altered soil properties and reduced plant-available water (Greacen and Sands 1980, Kozlowski 1999, Gomez et al. 2002). This could potentially increase plant water stress, leading to dieback and mortality. Hence, this issue needs to be researched further. Additionally, a more detailed examination of individual tree or species differences in physiology (i.e. measurements of stomatal conductance before and after VR, measurements of distal branch cavitation) may help to understand the differential responses to changes in microclimate.

- Many people believe that open-grown trees will benefit from the greater levels of light, water and nutrients available after removing neighbouring/competing trees (Wang et al. 1995, Liu et al. 2003). However, my study showed strongly elevated mortality rates of residual trees for 5 years after VR harvesting. Additionally, the observation of a large proportion of living residuals with heavy crown dieback suggests that the mortality likely continued for several more years after my study had been completed. Thus, it would be advantageous for land managers to have some idea of how long the mortality rates will remain elevated after VR. Similarly, it would be valuable to possess a better understanding of how long it may take before residual trees begin to benefit from the reduced competition after VR.
- Results from my research on carbon isotope discrimination suggest that residual trees in drier regions are suffering greater water stress than trees in wetter regions (Figure 4-1). While I have speculated that residual trees in drier regions may be more susceptible to dieback and mortality owing to their previous water stress, it is unclear whether this is the case. It could be argued that residual trees in mesic regions could be more vulnerable to cavitation following VR, because they have poorly developed drought tolerance compared to trees in more arid zones (Sparks and Black 1999, Rood et al. 2000). Consequently, an analysis of embolism and a mortality survey of VR harvested sites should be repeated in regions with different climatic regimes and

with additional species. This will help determine if elevated mortality may only be a concern in drier regions or if it is a potentially widespread problem for land managers in all regions.

- Owing to the potential for strongly elevated mortality rates of residual trees, it may be necessary for wildlife biologists and ecologists to analyse and reconsider whether the practice of VR harvesting with isolated residuals will provide adequate structure to meet certain objectives (e.g. to provide critical habitat elements for lifeboating species and processes, to enhance connectivity for movement of organisms, or to sustain basic ecosystem functions). Thus two basic questions should be answered: 1) Do these isolated residual trees survive; and 2) Do these isolated lifeboat trees provide the desired value(s) to meet the management objectives?
- If natural disturbances are used as the guide for our current forest management decisions, it is imperative to understand how natural and anthropogenic disturbances compare (Niemelä 1999). Therefore, we need more long-term empirical research comparing the post-VR harvest response to the post-fire response of residual trees. Three fundamental questions to be addressed are: 1) Do post-fire isolated trees in natural systems have higher mortality rates than background levels; 2) Do VR residuals have a higher rate of mortality than the post-fire residual trees?; and 3) How does the ecophysiological response of post-fire residuals compare to the post-VR response?
- Related to the conceptual framework presented above, an additional question arises. How does VR compare to other disturbances? Comparisons between the outcomes of VR and disturbances such as insect outbreaks, wind storms, ice storms, snow

breakages, tornadoes, or diseases could provide important insights into the most appropriate approach to implementing VR in regions most affected by these other disturbances.

- Additional research to determine if trees in patches are more likely to suffer less water stress and survive than isolated residuals is necessary. Currently, there is little reliable empirical data comparing the responses of residual trees in dispersed and aggregated retention. Additionally, the scientific literature is lacking in comparisons of the relative values of dispersed and aggregated retention. This quantitative information will be vital for land managers to make decisions about sustainability in terms of the desired retention levels and spatial patterns to achieve various objectives.
- Finally, I have shown that the majority of white spruce retained in VR cutovers died due to windthrow. However, it remains uncertain about the role of certain factors such as topographic relief, slope position, or soil type in this type of mortality in VR sites.

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Table 5-1. The likely dominant outcome for several boreal mixedwood tree species if retained as dispersed residuals following variable retention harvesting. Dominant VR outcome based on known embolism risk, windthrow risk, and rooting depth and/or morphology.

Species	Dominant VR Outcome[1]	Embolism risk	Ψ_{50} (MPa)[2]	Windthrow Risk	Rooting Depth (cm) and/or Morphology	References
Abies balsamea (L.) Mill.	SD, DWD	High	-2.1 to -2.5	High	< 75; root system typically confined to duff and upper mineral soil layers	Tyree and Sperry 1989, Sperry and Tyree 1990, Frank 1990, Tyree and Ewers 1991, Meunier et al. 2002, Achim et al. 2005
Betula papyrifera Marsh.	SD	High	-1.6 to -2.5	Low - Moderate	< 60; often shallow	Safford et al. 1990, Sperry et al. 1994
Larix laricina (Du Roi) K. Koch	SD, DWD	Moderate	-	Low - Moderate	20 - 45; roots commonly spread over areas greater in radius than the tree height	Lieffers and Rothwell 1987, Burns and Honkala 1990, Sperry et al. 1994
Picea engelmannii Parry ex Engelm.	DWD	Low - Moderate	-	Moderate - High	shallow; vertical sinkers to 240 in deep, porous, well-drained soils	Alexander and Sheppard 1984, Alexander 1987
Picea glauca (Moench) Voss	LL, DWD	Low	-3.7 to -4.0	Moderate - High	90 - 120; can develop taproots or sinker roots up to 300	Nienstaedt and Zasada 1990, Sperry et al. 1994, Meunier et al. 2002
Picea mariana (Mill.)	DWD	Low - Moderate	-	High	< 20; shallow and widespreading	Strong and La Roi 1983, Viereck and Johnston 1990, Blake and Li 2003, Elie and Ruel 2005
Pinus banksiana Lamb.	LL	Low	-	Low - Moderate	laterals < 45; taproot to 270	Rudolph and Laidly 1990, [illegible] et al. 1997, Blake and Li 2003, Elie and Ruel 2005
Pinus contorta Dougl. ex Loud.	LL, SD	Moderate	-2.4 to -2.8	Low	120; profuse development of vertical sinkers from lateral roots	Lotan and Critchfield 1990, [illegible] et al. 1996, Koch 1996, [illegible] et al. 2001
Populus balsamifera L.	SD	High	-1.6 to -1.8	Low - Moderate	shallow, spreading root system	[illegible] and [illegible] 1986, Tyree et al. 1994
Populus tremuloides Michx.	SD	Moderate - High	-2.2 to -3.0	Low - Moderate	shallow with widespread laterals; vertical sinkers to 270	Gifford 1966, Sperry et al. 1991, Sperry et al. 1994, Tyree et al. 1994
Pseudotsuga menziesii (Mirb.)	LL, SD	Low - Moderate	-2.3 to -4.0	Low	60 - 130; "plastic" morphology where growth unimpeded	[illegible] and [illegible] 1958, Burns and Honkala 1990, [illegible] 1992, Sperry and [illegible] 1997, Domec and Gartner 2001, Domec and Gartner 2002

[1] Abbreviations: LL: living legacy; SD: standing dead (snag); DWD: dead woody debris

[2] Ψ_{50}: xylem water potential at which the plant has reached 50% loss of hydraulic conductivity